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M. A. B. Fakorede
University of Ife

J. J. Mock
Northrup King Co.

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Correlated Responses to Recurrent Selection for Grain Yield in Maize

M. A. B. Fakorede and J. J. Mock
Department of Agronomy

Agriculture and Home Economics Experiment Station
Iowa State University of Science and Technology
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Summary

Experiments were conducted in three field environments with the following objectives: (1) to evaluate the progress from seven cycles of reciprocal recurrent selection in Iowa Stiff Stalk Synthetic [BSSS(R)] and Iowa Corn Borer Synthetic #1 [BSCB1(R)] and six cycles of half-sib family selection in 'Alph' (i.e., BS12) maize (*Zea mays* L.) populations, (2) to compare the response of unimproved and improved maize variety hybrids to different levels of nitrogen fertilizer and plant density, and (3) to evaluate the influence of nitrogen and plant density on the morphological and physiological traits associated with recurrent selection for grain yield in maize. Each experiment was grown in randomized complete blocks with a split-split-plot arrangement and two replications. Nitrogen fertilizer levels (0, 90, 180, and 270 kg N/ha) were main plots, plant densities (39,500; 59,300; 79,000; and 98,800 plants/ha) were subplots, and five variety hybrids, BSSS(R)C0 x BSCB1(R)C0, BSSS(R)C5 x BSCB1(R)C5, BSSS(R)C7 x BSCB1(R)C7, BS12C0 x B14A, and BS12C6 x B14A, were randomized as sub-subplots. We obtained data on grain yield and grain-yield components, flowering traits, plant traits, leaf area, leaf orientation, lodging, dry-matter productivity, and harvest index.

Recurrent selection significantly improved grain yields of the population cross of BSSS(R) and BSCB1(R) and of BS12 x B14A. Progress from seven cycles of reciprocal recurrent selection was positive and linear at 2.06 q/ha (i.e., 5.21%) per cycle. Observed mean difference between the C0 and C6 of the half-sib program indicated an average gain of 2.25 q/ha (or 6.00%) per cycle of selection in BS12. These results compare favorably with those previously reported for the first five cycles of selection in both programs.

Hybrids in our study demonstrated curvilinear responses to fertilizer nitrogen, with 180 kg N/ha being optimum for the hybrids from the reciprocal recurrent selection program and 90 kg N/ha being optimum for BS12C0 x B14A. BS12C6 x B14A, however, produced maximum yields at 270 kg N/ha. Improved hybrids consistently outyielded their unimproved counterparts at all nitrogen fertilizer levels we investigated.

Responses of the hybrids to increased plant density were linear and negative. Improved hybrids were superior to unimproved hybrids at all plant densities. Regression coefficients indicated that the C5 x C5 and C7 x C7 of the reciprocal recurrent selection program demonstrated greater ability to tolerate high plant densities than did the other hybrids.

Multiple-regression models involving linear, quadratic, and interaction terms were used to predict the response of grain yield to combinations of nitrogen fertilizer and plant density. Each hybrid demonstrated a quadratic response to nitrogen, but the linear b-value for nitrogen usually was larger than the quadratic b-value. Regression coefficients associated with plant density were negative, small, and nonsignificant. We concluded that, for the genotypes in our study, grain yield was affected primarily by nitrogen, and the linear response to nitrogen was more important than the quadratic. Optimum density was 39,500 plants/ha for each hybrid, but differences existed among hybrids for amount of nitrogen required to attain maximum yields at this plant density.

Generally, grain-yield components demonstrated significant, positive correlated responses to recurrent selection for grain yield. Magnitudes of these associations were large for number of ears per 100 plants and percentage of kernel moisture at harvest, but were rather small for other yield components. Most yield components increased as nitrogen rates increased, and decreased as plant density increased.

Dates of anthesis for improved and unimproved hybrids differed by approximately 1 day, but improved hybrids reached incipient silk extrusion several days earlier than did unimproved hybrids. Consequently, pollen-shed-to-silking interval was larger for unimproved than improved hybrids. Anthesis, days to silk emergence, and pollen-shed-to-silking interval decreased as nitrogen rates increased, and increased as plant density increased.

Expression of ear height, plant height, ear-height-to-plant-height ratio, number of tassel branches, and percentage of lodged plants increased as nitrogen rates increased. Plant density did not affect ear height, plant height, or lodging, but the number of tassel branches decreased with increased density. Effect of plant density on ear-height-to-plant-height ratio was small. Ear height did not change, but plant height increased with recurrent selection for grain yield. Consequently, ear-height-to-plant-height ratio decreased for the improved hybrids. Also, improved hybrids produced smaller tassels than did unimproved hybrids. BSSS(R)C7 x BSCB1(R)C7 demonstrated greater ability to resist lodging than did the C0 x C0 and C5 x C5 of these populations. Differences for lodging between the C0 and C6 of the half-sib program were not significant statistically.

Number of leaves per plant, area of ear leaf, leaf area per plant, leaf-area index, and grain per unit of leaf area increased with increased nitrogen rates; however, 90 to 180 kg N/ha was optimum for the expression of these traits. Leaf-area index increased as plant density increased, but values for other leaf-area traits decreased as plant density increased. All leaf-area traits increased significantly in the improved relative to the unimproved hybrids. We hypothesized that total canopy photosynthesis was greater for the improved than for the unimproved hybrids. The increased photosynthate produced by the improved hybrids, however, was used for filling more ears rather than for increasing kernel size. Yield increases for improved hybrids, therefore, resulted largely from increased ear number.

Leaf-orientation values indicated that improved hybrids possessed more upright canopies than unimproved hybrids. Orientation of the upper canopy in-

creased as nitrogen rates increased from 0 to 90 kg/ha. Nitrogen rates did not produce significant effects on orientation of the lower canopy. Orientation of the lower canopy increased, but that of the upper canopy did not change, as plant density increased.

Dry-matter productivity and harvest index increased significantly with increased nitrogen rates; however, differences for these traits among levels of nitrogen higher than 90 kg/ha usually were not significant. Increased plant density resulted in decreased dry matter per plant, decreased dry matter per unit of leaf area, and reduced harvest index.

Differences between plant densities for total dry-matter productivity (i.e., dry matter per hectare) were not significant. This result probably occurred because increased leaf-area index nullified the adverse effect of increased plant density on dry matter per plant. Hybrids from advanced cycles of selection demonstrated superior abilities to produce dry matter per plant, total dry matter, and dry matter per unit of leaf area. Also, harvest index increased markedly for the improved hybrids.

We concluded that the increased grain productivity associated with recurrent selection in BSSS(R) x BSCB1(R) and BS12 resulted from increased amounts of photosynthetically active leaf area, increased production of photosynthate, and increased translocation of photosynthate from source to sink.

Correlated Responses to Recurrent Selection for Grain Yield in Maize[1]

by M. A. B. Fakorede and J. J. Mock[2]

In the last three or four decades, plant breeders have developed breeding methods that have resulted in increased maize (*Zea mays* L.) grain yields in the United States. One of these breeding methods is recurrent selection, a cyclic process involving evaluation of a large number of genotypes from a population, identification and selection of a certain percentage of desirable genotypes, and recombination of the selected genotypes to form a new population from which further selections can be made. Recurrent selection is an effective method for increasing the frequency of favorable alleles for a quantitatively inherited trait without the rapid approach to homozygosity that often limits progress from selection in systems involving inbreeding.

Recurrent selection programs for improved grain yield were initiated in the 1940s and 1950s in several maize populations at the Iowa Agriculture and Home Economics Experiment Station. Seven cycles of reciprocal recurrent selection in Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1), and six cycles of recurrent half-sib family selection in 'Alph' (i.e., BS12), an open-pollinated variety, have been completed. Inbred B14 was the tester variety in the half-sib program. Although grain yield was the primary selection criterion, some attention was given to selection for lodging resistance and improved agronomic traits in later cycles of both programs. The original populations (C0) were selected under manure and legume crop rotation systems. Average amounts of nitrogen in the manure were estimated at 50 to 60 kg/ha, and plant densities were 30,000 to 35,000 plants/ha. By 1973, when the latest versions of the populations (C6 or C7) were developed, 160 kg N/ha and about 50,000 plants/ha were the average rates.

Our objectives in the research summarized herein were: (1) to evaluate the progress that resulted from recurrent selection for grain yield in the reciprocal recurrent selection and half-sib programs, (2) to compare the response of unimproved and improved maize populations to different levels of nitrogen and plant density, (3) to test the hypothesis that selection of maize genotypes under one type of environment will result in changes in performance of these genotypes in other environments (nitrogen and plant-density levels were the only environmental factors studied), (4) to evaluate changes in morphological and physiological traits associated with recurrent selection for grain yield, and (5) to evaluate the influence of nitrogen fertilizer and plant density on these correlated traits.

Studies of correlated traits are of interest to breeders for several reasons. They provide information on the genetic relationships between traits, the type of simultaneous change (negative or positive) that selection for one trait could promote in another (unselected) trait, and the relationship between a quantitative trait and fitness under natural selection. The first two reasons are important in the choice of traits that could be used to construct indexes for simultaneous improvement of two or more traits in a selection program. Furthermore, results obtained in studies of correlated traits often can be related to cytogenetic studies to determine whether two traits are associated through linkage or pleiotropism.

Review of Literature

Recurrent selection

The term "recurrent selection" was first used by Hull in 1945, although breeding systems with essentially the same concept were suggested by Hayes and Garber (1919) and East and Jones (1920). Studies on early testing for general combining ability in maize (Jenkins, 1940) showed that high-yielding inbred lines could be identified in early generations. On the basis of his results and on the assumption that yield heterosis was due to dominant favorable alleles, Jenkins (1940) outlined a breeding procedure for the production of synthetic varieties from short-time inbred lines. This procedure uses a broad-based tester and is called recurrent selection for general combining ability.

Hull (1945) noticed that yields of F_1 hybrids commonly exceeded the sums of yields of their inbred parents by more than 20%. He suggested overdomi-

[1]Project 2152, Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa. Portion of a dissertation submitted by the senior author in partial fulfillment of requirements for the Ph.D. degree.

[2]Univ. of Ife, Nigeria/USAID Joint Project Participant and Predoctoral Research Assistant (now Senior Lecturer, Department of Plant Science, Univ. of Ife, Ile-Ife, Nigeria) and Professor of Plant Breeding (now Director of Corn Research, Northrup King Co., Stanton, MN), respectively, Agronomy Department, Iowa State University, Ames, IA.

nance as the cause of this yield heterosis; therefore, the heterozygous condition would be more favorable than the homozygous condition at each locus. Consequently, Hull (1945) designed a breeding plan that would be fully effective for improving traits conditioned by overdominance. Because this procedure utilizes a narrow-based tester, it has been termed "recurrent selection for specific combining ability."

Crow (1948, 1952) presented theoretical evidence showing that maximum increase in hybrid vigor under the dominance hypothesis would be 5.0%. Heterosis greater than 5.0% of the mean of random breeding populations, therefore, could not be explained exclusively on the basis of simple dominance. He suggested other types of gene action, such as the interaction of nonallelic genes (i.e., epistasis) or heterozygote superiority to both the dominant homozygote and the recessive homozygote (i.e., overdominance) as a basis for heterosis.

Because of the controversy over the type of gene action involved in yield heterosis, quantification of variability in plant populations promoted an urgent need for designing effective breeding programs (Frankel, 1947). Previously, Wright (1921) had defined three types of genetic variances: (1) additive genetic variance (σ_a^2), (2) variance due to dominance deviations from the additive scheme (σ_d^2), and (3) variance due to deviation from the additive scheme resulting from the interaction of nonallelic genes (i.e., epistasis = σ_i^2). Although Wright (1935) initially outlined procedures for estimating genetic variances, they were first applied to maize breeding by Comstock and Robinson in 1948. Mating Designs I, II, and III for estimating genetic variances originated from the studies of Comstock and Robinson (1948, 1952). Furthermore, these authors presented a method for estimating the average degree of dominance (i.e., the relative proportion of the dominance variance to the additive variance) of genes.

Robinson et al. (1949) found that estimates of the average degree of dominance for genes conditioning grain yield in maize were in the overdominance range. These authors and Comstock and Robinson (1948) noted that linkage could cause genetic behavior similar to overdominance. Furthermore, even though there was overdominance at some loci, partial dominance could predominate at others. In view of this situation, Comstock et al. (1949) proposed a breeding method that would be effective regardless of type of gene action. This method is now known as "reciprocal recurrent selection."

Several other methods of recurrent selection have been proposed. Details of these methods were reviewed by Penny et al. (1963), Moll and Stuber (1974), and Sprague and Eberhart (1977).

Recurrent selection has been used extensively to improve important agronomic traits of various crops including maize. We will review, however, only the literature relevant to the methods (i.e., reciprocal recurrent selection and half-sib selection) evaluated in our studies.

Preliminary data obtained from a half-sib program in the open-pollinated variety Krug (using the single-cross tester, WF9 x M14) were discussed by Lonnquist (1961). The population x tester cross showed an increase in grain yield of 3.4% per cycle from C0 to C2. Concurrent experiments were conducted in Florida (Horner et al., 1963) to compare three methods of recurrent selection for enhanced grain yield of maize. The three methods were: (1) recurrent selection for specific combining ability using an inbred-line tester, (2) recurrent selection for general combining ability using the broad-based parental population as tester, and (3) selection based on S_2-line performance *per se*. The source population for the three programs was Florida 767. Evaluation of the three programs after five cycles of selection (Horner et al., 1973) showed significant linear increases in general combining ability of the populations for all three methods, but the inbred-tester method was significantly more effective than the other two methods (4.4% gain per cycle, compared with 2.4 and 2.0% for the broad-based tester and S_2-progeny methods, respectively). Horner et al. (1973) concluded that, because the inbred tester used in their study was homozygous recessive at many important loci, it was more effective in selecting dominant, favorable alleles than the broad-based tester, which probably had intermediate gene frequencies at most loci.

Seven cycles of recurrent selection for specific combining ability with a single-cross tester (F44 x F6) were evaluated by Horner et al. (1976). The source population was composed of the F_2 generation of a cross (GT112 x L578) and FS767, a broad-based composite. The seven cycles of selection resulted in 18% (i.e., 2.6% per cycle) more grain yield, 9% lower ear height, and 35% less lodging relative to C0.

Two recurrent selection programs of the type proposed by Sprague and Miller (1950) were conducted with maize in Iowa. Lancaster Surecrop and Kolkmeier were the unrelated heterozygous source populations used in the first program. A single-cross hybrid, WF9 x Hy, was the tester for the first cycle, and the inbred, Hy, was the tester for subsequent cycles (Sprague et al., 1959). After five cycles of selection (Walejko and Russell, 1977), rate of gain for yield was not significant for the Kolkmeier population *per se*; but a significant and negative rate was observed for the Lancaster population *per se*. Rates of gain for grain yield observed for the population crosses (i.e., C0 x C0 to C5 x C5) and population x Hy testcrosses were linear and significant. Gains in grain yield were expressed equally well when the populations were testcrossed to unrelated testers.

In the other program, 'Alph,' an open-pollinated variety, and (WF9 x B7)F_2 were the heterozygous stocks, with inbred B14 as the common tester (Penny et al., 1962). Russell et al. (1973) conducted a comprehensive evaluation of five cycles of selection from this program and observed significant grain-yield improvements in the populations *per se*, population crosses, and testcrosses of the populations to unrelated testers.

Results of long-term experiments in Kenya (East Africa), North Carolina, and Iowa demonstrated that reciprocal recurrent selection was effective in improving grain yield of maize. Two populations, KII and Ec573, were improved by reciprocal recurrent selection in Kenya. Three selection cycles in this program resulted in gains of 3.5% per year for the population crosses (Darrah et al., 1978). Number of ears per 100 plants increased also. Moll and Stuber (1971) evaluated six cycles of reciprocal recurrent selection in two open-pollinated varieties, Jarvis and Indian Chief. Significant increases in yield were observed for Jarvis (4.43 g/plant per cycle) and the variety cross (9.76 g/plant per cycle), but not for Indian Chief. Evaluation of progress from five cycles of reciprocal recurrent selection in Iowa Stiff Stalk Synthetic [BSSS(R)] and Iowa Corn Borer Synthetic #1 [BSCB1(R)] maize populations indicated that the improvement in yield of the population cross was linear and was 2.73 q/ha (4.6%) per cycle (Eberhart et al., 1973). No significant changes, however, were detected in the populations *per se*. Also, mid-parent heterosis for grain yield increased from 15% in the C0 x C0 to 37% in the C5 x C5 crosses of BSSS(R) and BSCB1(R). No changes were detected for ear height and maturity, but ears per 100 plants increased and lodging decreased in both populations and their cross.

Correlated responses to recurrent selection

Polygenic inheritance is dependent upon many genes that have similar, small effects. Therefore, selection applied to one polygenic trait almost always leads to changes in others. When selection is applied to trait X, associated changes in the unselected trait, Y, are known as correlated responses. Correlated responses may be either obligate or facultative (Lerner, 1958). Obligate correlated responses are particularly important when they result in decreased fitness. Facultative types of correlated responses affect certain traits in one selection program and different traits in another. Lerner (1958) suggested that facultative correlated responses occur because of differences in combinations of alleles in one population relative to the other. For example, combinations of alleles with a net "plus" effect on character Y may be linked with plus-acting alleles for character X in one population and with "minus" alleles in another. In such a case, selection to improve the mean performance of X in the two populations will be accompanied by correlated responses of Y in the opposite direction.

Several genetic mechanisms have been proposed as causes of correlated responses. The first mechanism is pleiotropy, the phenomenon by which a gene influences two or more traits simultaneously (Falconer, 1960). Correlations caused by pleiotropy may occur when the phenotypic expression of the traits is dependent upon alleles with general effects on metabolic efficiency, or upon the same hormone or enzyme systems. Linkage disequilibrium is another proposed cause of correlated responses. Linkage may hold existing gene combinations (either among similar or dissimilar alleles) together. It may be present in the original population or it may be generated by selection. Wigan and Mather (1942) suggested that, if genes controlling metric characters are organized in blocks, the polygenes concerned with the variability of one trait are intermingled along the chromosome with those that determine variability for another trait. Selection for increased frequency of certain blocks also will affect the frequencies of dissimilar alleles intermingled with these blocks, thereby resulting in correlated responses.

Many experiments designed to evaluate various selection methods have concentrated on single traits. Correlated changes in other traits, however, have been studied in several selection programs. Moll and Robinson (1966) reported observed and expected correlated responses to recurrent selection for grain yield in maize. They found good agreement between observed and expected correlated responses for number of ears per plant. Correlated responses for ear height and days to tasseling were not consistent. Four cycles of recurrent selection for reduced ear height in two maize populations resulted in significant reductions of plant height and grain yield (Acosta and Crane, 1972). Grain yield of a maize population increased at the rate of 6.3% per cycle through indirect selection for number of ears per plant (Lonnquist, 1967). Direct selection for grain yield in this variety (Gardner, 1961) showed a gain of only 3.8% per cycle. Other studies of recurrent selection in maize (Harris et al., 1972; Russell et al., 1973; Horner et al., 1976; Darrah et al., 1978) also demonstrated consistent, positive associations between grain yield and number of ears per plant. Correlated responses of other traits with selection for grain yield were inconsistent. Three cycles of recurrent selection for stalk-rot resistance resulted in correlated responses for 11 other traits (Jinahyon and Russell, 1969). In this study, grain yield showed a positive correlated response with improved stalk-rot resistance.

Effects of nitrogen fertilizer and plant density on maize growth and productivity

Plant breeders often are faced with the problem of determining the type of environment in which to practice selection. An ideal environment should enhance the heritability of traits being selected, as in the case of disease resistance under an artificial epiphytotic. Performance of genotypes in the selection environment should correlate highly with their performance across the range of environments in which they are to be used. According to Russell and Teich (1967), two views often expressed in the literature are:

(1) Selection for yield should occur under a high-productivity, or nonstress, environment so that genotypes being evaluated will demonstrate their optimum potential for yield. This model assumes that superior genotypes in high-productivity environments will be superior in other environments.

(2) Because the environment usually is suboptimal, crops should be developed for performance under stress conditions. Genotypes selected under

"better-than-normal" environments may be unadapted to the average range of environmental conditions under which the genotypes will be grown commercially. Application of some form of stress in the selection nursery or yield trials might alleviate this situation.

For the U.S. Corn Belt, amount of nitrogen fertilizer in the soil and level of plant density are two important environmental factors in commercial production of maize. Herein, we will review the literature on differential response of maize genotypes to nitrogen fertilizer and plant density levels.

McVicker and Shear (1946) studied three open-pollinated varieties and three hybrids of maize at five plant densities ranging from 9,633 to 48,412 plants/ha. Significant differences occurred for grain yield among the genotypes at each density. Optimum densities were 19,266 plants/ha for the open-pollinated varieties and 38,232 plants/ha for the hybrids. Lang et al. (1956) evaluated nine single-cross hybrids at six plant densities ranging from 9,900 to 59,300 plants/ha and three nitrogen fertility levels designated low, medium, and high. Differential yield levels were observed in the experiments. Single-cross hybrid, WF9 x C103, which had the best yields at the low densities, had the poorest yields at high plant densities. Contrarily, Hy2 x Oh7, which was one of the poorest yielders at low plant densities, had the highest yields at high plant densities. Additionally, Lang et al. (1956) observed that hybrids with a tendency to be multiple-eared at low densities had the lowest percentage of barren stalks at high densities. In another study involving a diallel of four inbred lines of maize, Woolley et al. (1962) found that all hybrid combinations with C103 resulted in the poorest yield responses to plant-density stress.

The relationship between second-ear development and genotype x density interaction in maize was investigated by Collins et al. (1965). Grain yields of 36 single-cross hybrids that were classified into three types (i.e., 1-ear x 1-ear, 1-ear x 2-ear, and 2-ear x 2-ear) were compared at approximately 20, 30, 40, and 50 thousand plants/ha at four environments (2 locations, 2 years) in central Iowa. The 2-ear[3] type produced higher yields across plant densities than did the 1-ear type. This relatively consistent performance of prolific x prolific hybrids was attributed to the capacity of these hybrids to adjust to environmental fluctuations by changing the numbers of ears produced. Collins et al. (1965) concluded that prolific genotypes may perform better than single-eared genotypes at high plant densities. Further studies (Russell, 1968) indicated that prolific hybrids produced their highest yields at 58,100 plants/ha, whereas optimum density for nonprolific hybrids was 38,700 plants/ha. Incidence of barren stalks at 58,100 plants/ha was 4X greater for nonprolific than for prolific hybrids. Although prolific hybrids had 27% stalks with second ears at the low density (29,000 plants/ha), second ears accounted for only 9.8% of their total yield. Also, Russell and Eberhart (1968) analyzed yield stability of prolific and nonprolific three-way crosses in two experiments, one with 12 environments (4 locations, 3 years) and the other with 24 environments (4 plant densities, 2 locations, 3 years). Comparisons of the stability parameters (i.e., mean yield, b-values, and deviation mean squares) indicated that prolific hybrids were more stable than nonprolific hybrids. Russell and Prior (1975) reported similar results for a different set of genotypes. Evidently, genotype x density interactions are greater for single-eared than for multiple-eared maize genotypes. Second-ear development, therefore, seems to be a mechanism that contributes to developmental homeostasis of U.S. Corn Belt maize.

Effects of plant density on the relationship between agronomic traits and grain yield of maize have been studied. El-Lakany and Russell (1971) evaluated ten low-yielding and ten high-yielding inbred lines (F_5 generation from M14 x C103) in six environments at 31.0, 40.8, and 59.5 thousand plants/ha. Only plant and ear heights were significantly correlated with yield ($r = 0.51$ and 0.47, respectively) at the low density; but at the intermediate density, plant and ear heights, ear diameter, and shelling percentage showed positive correlations with grain yield. At the high plant density, however, all traits except 300-kernel weight and dates of pollen shed and silk emergence were correlated significantly with yield. Except for pollen-shed-to-silking interval ($r = -0.66$), all significant r-values were positive. Studies by Mock and Buren (1972) and Buren et al. (1974) indicated that density-tolerant maize genotypes were characterized by rapid completion of silk extrusion, coincidence of pollen shed and silk extrusion, rapid growth of the first ear and first-ear silk, prolificacy, small tassel size, and efficient production of grain per unit leaf area.

Several investigations have shown that genotypic response of maize to plant density may vary with the fertility level of the soil. A study conducted for 11 years at two fertility levels (manure and no manure) with four plant density levels within each fertility level (Mooers, 1933) indicated differential responses of maize genotypes to fertility and plant-density combinations. Highest yielders under poor conditions (no manure, high planting rates) were not the highest yielders under low-density, high-fertility conditions. Mooers (1933) suggested the use of various fertility and density levels in yield trials for maize. Duncan (1954) found that fertility and density levels adequately explained the differences in yielding capacity of three hybrids. At low fertility levels, differences in yield at any stand level were very small, but as plant density and fertility levels increased, the spread in yields of the hybrids became more pronounced. Duncan (1954) pointed out that, to make a critical study of optimum soil fertility levels for maize genotypes, plant density should be high enough to exert a near-maximum demand on the fertility resources of the soil.

[3]Hereafter, "prolificacy" will be used to describe ability to produce two or more ears.

Russell and Teich (1967) selected two groups of maize lines, one under low plant density, the other under high plant density. When hybrid performances of the two groups were compared at density levels ranging from 29.6 to 69.2 thousand plants/ha, there were no significant yield differences between the two groups within and across plant densities. These results indicated that selection at low or high densities produced lines with similar responses to plant density levels. Regression of yield on density, however, produced smaller negative b-values for the group selected under dense stand, indicating that a lower yield reduction was associated with density stress for lines selected under high-density conditions. In a subsequent study, Russell (1969) selected inbred lines for three generations at a low (38,700 plants/ha) or a high (58,100 plants/ha) plant density. When the resulting S_3 lines were evaluated in testcrosses with a double-double-cross tester, both groups of lines yielded similarly at low densities (29.1 to 32.2 thousand plants/ha). At medium and high densities (43.6 to 64.4 thousand plants/ha), however, testcrosses of the high-density group outyielded those of the low-density group. Differences in yield at these densities resulted from a greater incidence of barren stalks in the low-density selections.

Two studies have been conducted in central Iowa to compare the relative performace of maize hybrids developed during different eras within the last 50 years. During this period, field husbandry (e.g., increased fertilizer use, increased plant density, better weed control) has improved gradually. Russell (1974) evaluated 25 genotypes (one open-pollinated variety, 16 double-cross hybrids, and eight single-cross hybrids) representing the period from 1930 to 1970. The genotypes were grown at 29.7, 44.5, and 59.3 thousand plants/ha in 12 environments (4 locations, 3 years). Generally, results showed an increasing trend for yield from the open-pollinated variety to the hybrids developed in 1970. Hybrids developed during later eras were more density tolerant than the open-pollinated variety and hybrids developed during earlier eras. Regressions of yield on density showed significant and positive linear b-values for hybrids developed during the era from the mid-1950s to 1970. Similar values for hybrids developed earlier were negative. Additionally, Russell (1974) found that hybrids from the 1960s or later were more stable in yield performance than hybrids developed earlier.

Duvick (1976) evaluated 19 commercial hybrids introduced during the period 1930 through 1971 at 32, 44, and 66 thousand plants/ha at four central Iowa environments (2 years, 2 locations). In a second experiment, Duvick (1976) evaluated 50 single crosses obtained from inbred lines introduced during the period from 1930 to the early 1970s. Six environments (3 locations, 2 years) and the density levels of the first experiment were used in the second experiment. In both experiments, the genotypes yielded similarly at the low plant density (commercial density of 1935). At the intermediate (average commercial density of 1975) and high plant densities, however, the newer the hybrid, the higher the grain yield. Highest yields for "old" and "more recent" hybrids were attained at 32,000 and 44,000 plants/ha, respectively. Furthermore, Duvick (1976) found that yield superiority of the new hybrids was closely associated with low amounts of root and stalk lodging at all densities, and low incidences of barrenness at the intermediate and high plant densities. Maturity and prolificacy of "old" and "new" hybrids were not different.

Arboleda-Rivera and Compton (1974) conducted three cycles of mass selection for yield and prolificacy of maize under wet (nonstress) and dry (stress) seasons in Colombia, South America. The four populations (C0 to C3) developed in each environment were evaluated for 3 years under the selection environment and the alternative environment. When tested in the wet season, wet-season selections showed improvements of 10.5 and 8.8% per cycle for yield and prolificacy, respectively. The corresponding figures were 0.8 and 1.0%, respectively, when wet-season selections were evaluated in the stress environment. Dry-season selections showed improvements of 2.5 and 4.4% per cycle for yield and prolificacy, respectively, when evaluated under dry-season conditions, whereas these gains were 7.6 and 11.4% when dry-season selections were evaluated under nonstress, wet-season conditions. Therefore: (1) selection for prolificacy under stress demonstrated greater gain than selection under nonstress conditions when evaluated in nonstress environments; (2) selections for prolificacy under nonstress conditions may not carry through when evaluated under stress conditions; and (3) selections for grain yield under stress resulted in greater gains than selections under nonstress when both were evaluated under stress conditions.

Although more studies on relative performance of genotypes selected under stress and nonstress conditions will be necessary before valid, general conclusions can be drawn, results of such studies reviewed herein suggest that: (1) genotypes selected under high fertility and high plant density levels tend to be stable in yielding ability at other levels of these two environmental factors; (2) selection made under "normal" season conditions may perform poorly under adverse growing conditions; and (3) maize genotypes to be grown commercially in high plant density or moisture-stress environments should be selected in these environments.

Materials and Methods

Production of variety hybrids for evaluation

Seed of BSSS(R)C0, BSSS(R)C5, BSSS(R)C7, BSCB1(R)C0, BSCB1(R)C5, BSCB1(R)C7, BS12C0, BS12C6, and B14A was removed from cold storage in 1974, and the following crosses were made: BSSS(R)C0 x BSCB1(R)C0, BSSS(R)C5 x BSCB1(R)C5, BSSS(R)C7 x BSCB1(R)C7, BS12C0 x B14A, and BS12C6 x B14A.

For each cross, a 17-plant row of one parent was paired with a 17-plant row of the other parent, and 10 pairs of rows were planted. Except for B14A, plants

were used only once, either as male or female parent, and efforts were made to cross as many plants in a row as possible. To minimize sampling error in the heterogeneous sources, at least 100 plants in each population were used in the preparation of a population cross. Seed from all ears of each cross was bulked and grown in our 1975 and 1976 evaluation experiments. Remnant seed from each cross was placed in cold storage.

Experimental procedures

The five variety hybrids were evaluated in three field environments (Bruner Farm, 1975 and 1976, and Ankeny, 1976), with four rates of nitrogen fertilizer (0, 90, 180, and 270 kg N/ha) and four plant densities (39.5, 59.3, 79.0, and 98.8 thousand plants/ha) in each environment. Urea (46.0% N) was the source of nitrogen. Each experiment was grown in a randomized-complete-block design with a split-split-plot arrangement and in two replications. Nitrogen rates were main plots, plant densities were randomized within N-levels as subplots, and hybrids were randomized within plant densities as sub-sub-plots. (Unless otherwise noted, hereafter sub-sub-plots will be referred to as plots.) Plots consisted of four rows, 5.88 m long and spaced 76 cm apart. Main plots were separated by four and eight 76-cm rows at the Bruner Farm and Ankeny, respectively. A commercial hybrid was planted in these rows to provide adequate competition. A 76-cm alley separated subplots. Nitrogen was hand broadcast on the treated main plots the day before planting at Bruner Farm in 1975 and immediately after planting in the other environments. Applied nitrogen was harrowed into the soil 1 day after application to minimize losses from volatilization. Also, approximately 90 kg/ha of P and K were plowed down during the fall preceeding each growing season. Experiments were hand planted on May 17, 1975, and May 11, 1976, at the Bruner Farm. One-fourth of the Ankeny experiment was planted on May 15, 1976, and, because of rainy conditions, the rest could not be planted until May 18, 1976. We overplanted all plots and subsequently thinned them to contain the desired plant densities. Weeds were controlled by preplant applications of Lasso (2.4 liters/ha) and by hand weeding.

The following data were recorded from one of the center two rows of each plot at Bruner Farm in 1975 and 1976:

Flowering dates: We recorded the dates when 50% of the plants in each plot attained anthesis (DPS; i.e., displayed dehiscent anthers at least halfway down the central tassel branch) and incipient silk extrusion (DSE), and these were expressed as days from July 1. Pollen-shed-to-silking interval (PSSI) was obtained by subtracting DPS from DSE.

Plant traits: At maturity, ear and plant heights of five competitive plants per plot were measured (in cm) from the soil surface to the node of the top ear (EHT) and to the collar of the flag leaf (PHT), respectively. Position of top ear relative to mature plant height (EHR) was obtained by dividing EHT by PHT. Number of green leaves per plant was recorded during grain filling for five plants in each plot. Also, we recorded total number of tassel branches (i.e., including the central tassel branch) for five random plants per plot.

Leaf area: We measured length (l) and maximum width (w) of leaves subtending top ears of five random plants in each plot and calculated ear-leaf area (ELA) by the formula (Montgomery, 1911):

$$ELA = 0.75lw$$

Leaf area per plant (PLA) was estimated by multiplying ear-leaf area by the leaf-area factor, 9.39, developed for Corn Belt maize genotypes by Pearce et al. (1975). Additionally, leaf area per plant was converted to leaf-area index (i.e., LAI = PLA × number of plants per unit of land area).

Leaf orientation values (LOV): During grain filling, measurements necessary to calculate leaf orientation values were taken on five plants per plot. Values for the leaf above (ALOV) and below (BLOV) the top ear were calculated by the formula (Pepper et al., 1977):

$$LOV = \sum_{i=1}^{n} A(L_{fp} / L_T)/n$$

where A = leaf angle (degrees from horizontal) at point of attachment of leaf blade to plant stem, L_{fp} = length (cm) of each leaf from the point of attachment to the point where it became parallel to the soil surface or "flagged" (i.e., "flagging point"), L_T = total length (cm) of each leaf, and n = number of leaves measured per plot (i.e., 5).

Lodging: Because a heavy rainstorm occurred early in September of 1975, it was impossible to distinguish effectively between root and stalk lodging. Therefore, number of plants in a plot that were leaning more than 45° from the vertical (visual rating), or were broken below the ear node was recorded in mid-September each year. This number was expressed as percentage of total plants per plot and served as an estimate of total lodging.

Dry-matter productivity: At approximately black-layer formation in 1975, six competitive plants from one of the center rows of each plot were cut near the soil surface, dried to constant moisture in a commercial grain drier, and weighed. In 1976, the six-plant sample was chopped into small pieces with a portable mechanical chopper (Diadem Brush Chipper, Model 316, Vandermolen Corp., Livingston, New Jersey), dried to constant moisture in a forced-air drier, and weighed. Weights were divided by number of harvested plants per plot to give dry matter per plant (DMPP) and expressed in grams. Total dry-matter (TDM) was determined by multiplying DMPP by

number of plants per plot, dividing by plot land area (i.e., 4.645 m^2), and converting to metric tons per hectare (t/ha).

Grain yield and grain-yield components: Ears (including dropped ears) were hand harvested from all plants (except those in the two end hills) in the center row that was not used for dry-matter determinations, and these ears were visually rated for percentage of cob covered with grain. Ears having less than 25% of their cobs covered with kernels were considered barren and discarded. The remaining ears were counted as harvestable ears. Number of harvestable ears was multiplied by 100 and divided by number of plants per plot (minus end hill plants) to give number of ears per 100 plants. Also, number of kernel rows (KRN), ear length (EL), ear diameter (ED), and cob diameter (CD) were recorded for five randomly selected ears per plot. Kernel depth (KD) was obtained by subtracting CD from ED. Harvestable ears per plot were shelled and weighed. Sample weights were divided by number of plants per plot to estimate average grain yield per plant (GRPP), and by plot land area to estimate total grain yield per land area (GYH). Total grain yield was converted to quintals per hectare. A 300-kernel sample was saved from each plot and weighed (KWT). Also, small samples of kernels from at least five competitive plants in a plot were composited for grain-moisture determination. Moisture percentage was determined with a Steinlite moisture tester in 1975 and with an electronic Moisture Tester (Dickey John) for the two experiments in 1976. Data for grain yield and grain-yield components were obtained from all three experiments.

Other parameters generated from these data were:

1. Grain yield per unit leaf area (GRPLA): GRPLA = (GRPP/PLA) × 100
2. Dry matter per unit leaf area (DMPLA): DMPLA = (DMPP/PLA) × 100
3. Harvest index (HI), the ratio of economic yield to total productivity: HI = (GRPP/DMPP) × 100

Statistical analyses

All environments were considered random, and data were combined across environments without partitioning out years and locations. Use of locations and years as random environments simplified the combined analysis of variance because there was one location in 1975 and two in 1976. All other factors (i.e., nitrogen, plant density, and hybrids) were considered fixed. We performed analyses of variance on all traits measured. Differences between means for main effects and interaction effects that showed significant F-tests were tested further by appropriate LSD values (Snedecor and Cochran, 1967).

In the analysis of variance for yield, degrees of freedom and mean squares for environments (E) and hybrids (H) were partitioned into relevant orthogonal components; i.e., Bruner Farm 1975 vs. Bruner Farm 1976 and Ankeny vs. others for environments; and reciprocal recurrent selection (RRS) vs. half-sib (HS); BS12C0 vs. BS12C6; C0 x C0 vs. C5 x C5, C7 x C7; and C5 x C5 vs. C7 x C7 for hybrids. Additionally, degrees of freedom and mean squares for nitrogen (N) and density (D), and their interactions with E, H, and with each other, were partitioned into linear, quadratic, and remainder components by using the procedure outlined by Steel and Torrie (1960).

The relationship between cycles of selection and grain yield was investigated for population crosses from the reciprocal recurrent selection program. This relationship could not be quantified for the half-sib program because of inadequate degrees of freedom. Estimates of regression coefficients for a linear model were obtained to determine the relative rate of gain per cycle of selection. The linear regression model that we used was:

$$\hat{Y}_{ij} = m + b_1 C_j + e_{ij}$$

where

$\hat{Y}_{ij}$ = predicted mean yield of the i^{th} population cross (C0 x C0, C5 x C5, C7 x C7) in the j^{th} cycle of selection (j = 0, 5, 7)
m = predicted value for the C0 x C0 cross
b_1 = linear regression coefficient
C_j = the j^{th} cycle of selection
e_{ij} = deviation from regression

The model was fitted to hybrid means obtained across and within environments.

Similarly, estimates of regression coefficients for linear and quadratic models were obtained for grain yield to determine the relative rate of change at each level of nitrogen and plant density. Again, the two models were fitted to hybrid means across and within environments. The linear model was:

$$\hat{Y}_{ij} = m_i + b_1 X_{ij} + e_{ij}$$

and the quadratic model was:

$$\hat{Y}_{ij} = m_i + b_i X_{ij} + b_q (X_{ij}^2) + e_{ij}$$

where

$\hat{Y}_{ij}$ = predicted mean yield at the j^{th} level of the i^{th} effect
m_i = predicted yield at the zero level of the i^{th} effect (nitrogen or plant density)
b_i = linear regression coefficient
b_q = quadratic regression coefficient
X_{ij} = j^{th} level of the i^{th} effect; j = 0, 1, 2, 3, for nitrogen, and j = 1, 2, 3, 4 for plant density
X_{ij}^2 = square of the j^{th} level of the i^{th} effect
e_{ij} = deviation from regression

Additionally, observed yield values were fitted to a multiple-regression model to develop response surfaces for the following situations: (1) grain yield averaged across all environments and hybrids, (2) mean

yields across all hybrids within environments, (3) mean yields of each hybrid across environments, and (4) mean yields of each hybrid within environments. The multiple regression model that we used was:

$$\hat{Y} = b_0 + b_1N + b_2D + b_3(N^2) + b_4(D^2) + b_5(ND)$$

where

$\hat{Y}$ = predicted grain yield
b_0 = predicted overall mean (intercept)
$b_1 - b_5$ = multiple regression coefficients
N = kg/ha of nitrogen
N^2 = kg/ha of nitrogen squared
D = plants/ha
D^2 = plants/ha squared
ND = interaction effects for nitrogen and plants/ha

Results and Discussion

Direct response to recurrent selection

Reciprocal recurrent selection has been effective in improving grain yield of the population cross of BSSS(R) x BSCB1(R). Estimated gain in grain yield was linear and was 2.1 q/ha (i.e., 5.2%) per cycle; a total gain of 14.4 q/ha for the seven cycles of selection. Observed mean difference in yield between C0 x C0 and C7 x C7 of these populations was 14.9 q/ha (Table 1). Rate of gain for the first five cycles of selection in this program was estimated at 2.7 q/ha (or 4.7%) per cycle, and observed yield difference between the C0 x C0 and C5 x C5 was 12.7 q/ha (Eberhart et al., 1973). The observed difference between the C5 x C5 and C7 x C7 (6.0 q/ha, Table 1) was highly significant (Table 2). Results obtained in our studies, therefore, showed that further progress from selection was made from C5 to C7 of the program.

Similarly, observed increase in grain yield of BS12 x B14A was 2.2 q/ha (or 6.0%) per cycle, and total gain of C6 relative to C0 was 13.5 q/ha (Table 1). Russell et al. (1973) observed a rate of gain of 2.9 q/ha (or 4.2%) per cycle for the first five cycles in this half-sib selection program.

Table 1. Mean grain yields of five maize variety hybrids in three environments.

Hybrid	Grain yield (q/ha)[†] Bruner Farm 1975	Bruner Farm 1976	Ankeny 1976	$\bar{X}$ Hybrid
BSSS(R) x BSCB1(R)				
C0 x C0	33.5	34.4	50.7	39.5
C5 x C5	39.2	43.3	62.7	48.4
C7 x C7	45.4	47.3	70.7	54.4
BS12 x B14A				
C0	29.9	30.2	52.1	37.4
C6	41.4	46.2	64.9	50.9
$\bar{X}$	37.9	40.3	60.2	

[†]$LSD_{.05}$ for environments = 10.93, for hybrids = 2.27, and for hybrids x environments = NS.

Table 2. Combined analysis of variance for grain yield of five variety hybrids grown in nitrogen-plant-density experiments.

Source	D.F.	Mean squares
Environments (E)	2	24134.1*
Bruner Farm 1975 vs 1976	1	778.4
Ankeny vs Others	1	47489.1**
Error a	2	516.5
Nitrogen rates (N)	3	11533.2***
N_{linear} (N_l)	1	27249.8***
$N_{quadratic}$ (N_q)	1	6697.6***
Remainder	1	652.2
N x E	6	916.2
N_l x E	2	1194.0
N_q x E	2	557.8
Remainder	2	996.8
Error b	9	486.1
Density (D)	3	6437.2***
D_{linear} (D_l)	1	19221.4***
$D_{quadratic}$ (D_q)	1	1.2
Remainder	1	89.0
D x E	6	147.0
D_l x E	2	255.5
D_q x E	2	150.5
Remainder	2	35.0
D x N	9	111.0
D x N_l	3	138.3
D x N_q	3	120.2
Remainder	3	74.8
D x N x E	18	122.2
Error c	36	109.8
Hybrids (H)	4	5188.7***
RRS vs HS	1	1273.6***
BS12C0 vs BS12C6	1	8709.2***
C0 x C0 vs C5 x C5, C7 x C7	1	9220.8***
C5 x C5 vs C7 x C7	1	1551.8***
H x E	8	112.7
H x N	12	91.8
H x N_l	4	203.4*
RSS vs HS x N_l	1	8.6
BS12C0 vs BS12C6 x N_l	1	759.1***
C0 x C0 vs C5 x C5, C7 x C7 x N_l	1	17.4
C5 x C5 vs C7 x C7 x N_l	1	28.3
H x N_q	4	25.0
Remainder	4	47.0
H x D	12	176.2**
H x D_l	4	438.7***
RSS vs HS x D_l	1	1140.1***
BS12C0 x BS12C6 x D_l	1	52.0
C0 x C0 vs C5 x C5, C7 x C7 x D_l	1	562.6**
C5 x C5 vs C7 x C7 x D_l	1	0.1
H x E x N	24	94.4
H x E x D	24	74.6
H x N x D	36	91.6
H x E x N x D	72	49.1
Error d	192	63.7

*, **, and *** Significant at 0.05, 0.01, and 0.001 levels of probability, respectively.

Table 3. Nitrogen x density interactions for observed and estimated rates of gain after seven cycles of reciprocal recurrent selection for grain yield in BSSS(R) and BSCB1(R).

		Gain per cycle														
		39,500†			59,300			79,000			98,800			$\bar{X}$ nitrogen		
kg N/ha		q/ha	% C0	R^2	q/ha	% C0	R^2	q/ha	% C0	R^2	q/ha	% C0	R^2	q/ha	% C0	R^2
0	Estimated	1.61	4.5	0.81	1.26	4.1	0.99	2.08	9.1	0.89	2.58	16.4	1.00	1.88	7.2	1.00
	Observed	1.80	4.9		1.27	4.1		1.90	8.7		2.59	16.4		1.89	7.5	
90	Estimated	1.94	3.9	0.92	2.21	5.4	0.92	2.69	8.0	0.97	2.08	6.0	0.97	2.23	5.6	0.98
	Observed	2.08	4.1		2.38	5.7		2.80	8.2		1.99	5.8		2.31	5.6	
180	Estimated	1.12	2.2	0.98	2.00	4.0	0.92	3.10	7.7	0.83	1.98	4.9	1.00	2.05	4.6	0.95
	Observed	1.07	2.2		2.15	4.2		3.45	8.3		1.99	5.0		2.17	4.8	
270	Estimated	0.89	1.5	0.89	1.59	3.2	0.57	2.58	6.4	1.00	3.24	9.8	0.99	2.08	4.6	0.98
	Observed	0.82	1.4		1.93	3.7		2.51	6.2		3.30	9.9		2.14	4.6	
$\bar{X}$ Density	Estimated	1.39	2.9	0.98	1.76	4.1	0.87	2.61	7.6	0.99	2.47	8.0	1.00			
	Observed	1.44	2.9		1.93	4.4		2.67	7.7		2.47	8.0				

†Plants/ha.

Response of the population cross of BSSS (R) and BSCB1(R) to reciprocal recurrent selection within nitrogen fertilizer levels, plant densities, and nitrogen x density interactions showed considerable variation in the rate of gain in grain yield. Highest rate of gain (and largest difference between C0 x C0 and C7 x C7) occurred under low-nitrogen, high-density conditions (Table 3). Evidently, grain-yield advantage of C7 x C7 over C0 x C0 was more pronounced as the environment became more stressed. Generally, progress from recurrent selection is evaluated in experiments conducted in several environments (i.e., locations and years), but usually at only one level of nitrogen fertilizer and only one plant density. Our results suggest that two or more rates of nitrogen and plant densities should be included in each environment where evaluation experiments are grown. Also, they demonstrated that superior maize genotypes selected under relatively high plant densities and high levels of fertilizer nitrogen outyielded those selected under low levels of these environmental factors, especially when both were evaluated under low-nitrogen, high-plant-density conditions. However, success from recurrent selection *per se* could be responsible for some of the differences observed.

Response surfaces for grain yield

Highly significant differences for grain yield occurred among N rates, and the linear component (N_{linear}) accounted for nearly 80% of the differences (Table 2). The significant quadratic effect ($N_{quadratic}$), however, indicated that a curvilinear relationship described the data better.

Regression of grain yields (averaged across environments, densities, and hybrids) on nitrogen fertilizer levels showed a curvilinear, positive response to increasing rates of nitrogen fertilizer, with maximum yield being attained at approximately 180 kg N/ha (Figure 1). Of all interaction mean squares involving nitrogen, only the H x N_{linear} was significant (Table 2). Consequently, the curvilinear response to increasing rates of nitrogen fertility observed for each hybrid (Figures 2 and 3) was consistent for all locations and plant densities.

On the average, BSSS(R)C7 x BSCB1(R)C7 produced from 33% (at 270 kg N/ha) to 50% (at 0 kg N/ha)

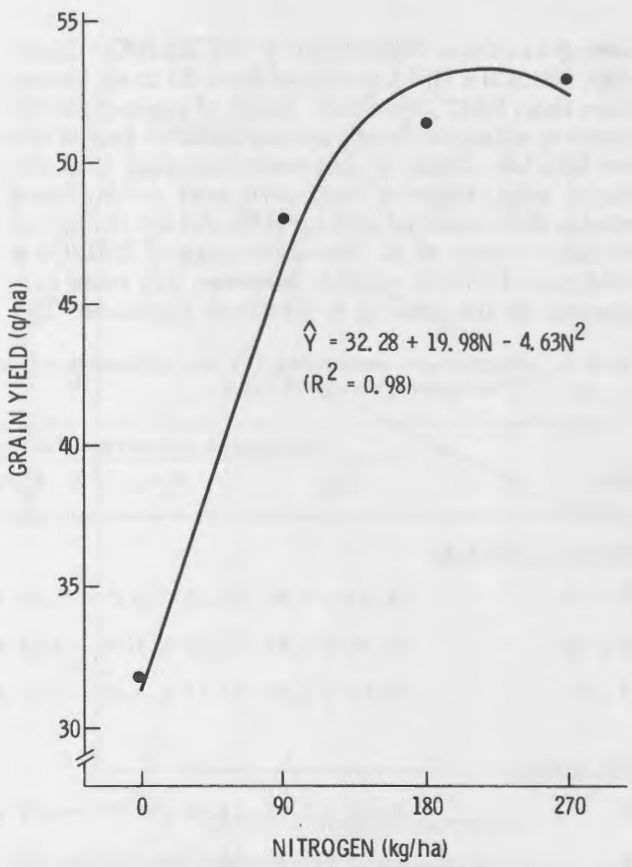

Figure 1. Predicted grain-yield response to nitrogen rates for five maize variety hybrids. Plotted points are observed yields.

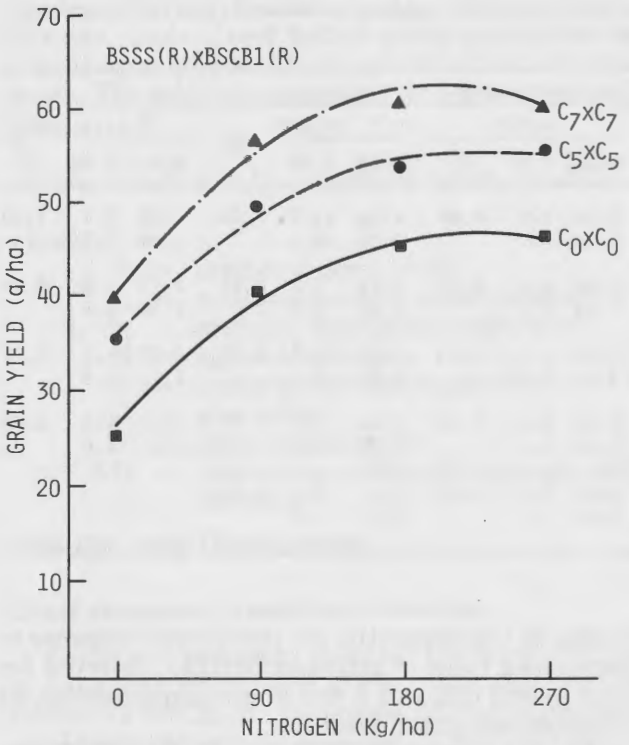

Figure 2. Predicted responses for variety hybrids of BSSS(R) x BSCB1(R) to nitrogen rates. Plotted points are observed yields.

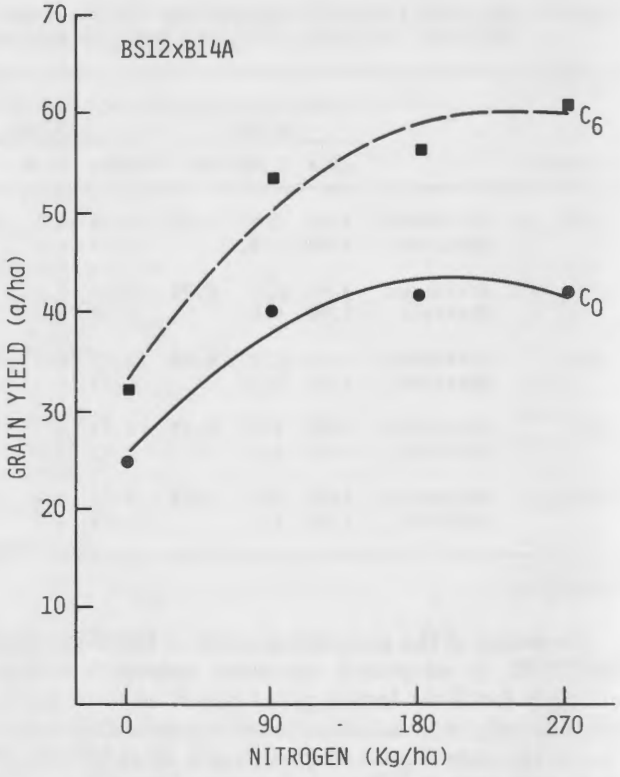

Figure 3. Predicted responses for variety hybrids of BS12 to nitrogen rates. Plotted points are observed yields.

more grain than BSSS(R)C0 x BSCB1(R)C0. Similarly, BS12C6 x B14A produced from 33 to 44% more grain than BS12C0 x B14A. Rates of grain-yield response to nitrogen (b-values) obtained for four of the five hybrids (Table 4), however, indicated that the initial advantages of improved over unimproved hybrids that occurred at 0 kg N/ha did not change at the other levels of N. The advantage of BS12C6 x B14A over BS12C0 x B14A, however, was more pronounced as the rate of N fertilizer increased. The significant H x N_{linear} resulted from this difference (Table 2). Evidently, BSSS(R)C5 x BSCB1(R)C5 and BSSS(R)C7 x BSCB1(R)C7 utilized N more efficiently than did BSSS(R)C0 x BSCB1(R)C0, but the efficiency did not change from 0 to 270 kg N/ha. We wish to caution, however, that variety hybrids are highly heterogeneous and that our results could have been confounded by environments and plant densities.

Table 4. Regression parameters for the influence of nitrogen (N) and plant density (D) on grain yield of five maize variety hybrids.

Hybrid	Regression parameters for nitrogen†				Regression parameters for plant density		
	b_0	b_1N	$b_2(N^2)$	R^2	b_0	b_1D	R^2
BSSS(R) x BSCB1(R)							
C0 x C0	26.53 ± 0.89	18.33 ± 1.59	-4.14 ± 0.56	0.997**	61.59 ± 2.68	-0.319 ± 0.04	0.974**
C5 x C5	35.98 ± 1.85	17.22 ± 3.30	-3.82 ± 1.17	0.985**	61.27 ± 1.69	-0.186 ± 0.02	0.970**
C7 x C7	40.02 ± 1.95	21.41 ± 3.48	-5.11 ± 1.24	0.987**	67.15 ± 1.95	-0.184 ± 0.03	0.959**
BS12 x B14A							
C0	25.61 ± 2.67	18.65 ± 4.77	-4.73 ± 1.69	0.964**	61.43 ± 0.95	-0.348 ± 0.13	0.997**
C6	33.27 ± 4.37	24.21 ± 7.81	-5.33 ± 2.77	0.959**	78.21 ± 3.26	-0.396 ± 0.05	0.975**
Hybrids combined	32.28 ± 2.35	19.98 ± 4.18	-4.63 ± 1.49	0.980**	65.93 ± 0.96	-0.286 ± 0.13	0.996**

†All b-values were significantly different from zero at 0.05 level of probability.

Overall yields of the hybrids in our studies showed a negative linear response to plant density (Table 4 and Figure 4). Observed and predicted values agreed closely, and addition of a quadratic term did not improve the linear model (Table 4). Evidently, the genotypes in our studies were intolerant of high plant densities. Highly significant H x D and H x D_{linear} interaction mean squares (Table 2), however, suggested that some of the variety hybrids were more tolerant of high plant densities than others. Clearly, BSSS(R)C5 x BSCB1(R)C5 and BSSS(R)C7 x BSCB1(R)C7 were more tolerant of high plant densities than were the other hybrids evaluated (Tables 2 and 4). Rates of decrease in grain yield associated with increased plant density were lower for these two hybrids than for the others. It should be noted, however, that the improved hybrids produced higher grain yields than their unimproved counterparts at all plant densities (Figures 5 and 6). As we mentioned previously, lines that were intermated to produce BSSS(R)C7, BSCB1(R)C7, and BS12C6 were selected under higher plant densities than those intermated to produce the C0 and C1 populations. These results, although confounded with success from selection *per se*, seem to indicate that selection of maize genotypes for performance at high plant densities should be practiced under high-density conditions. Results from studies by Russell (1969, 1974) and Duvick (1976) produced similar conclusions.

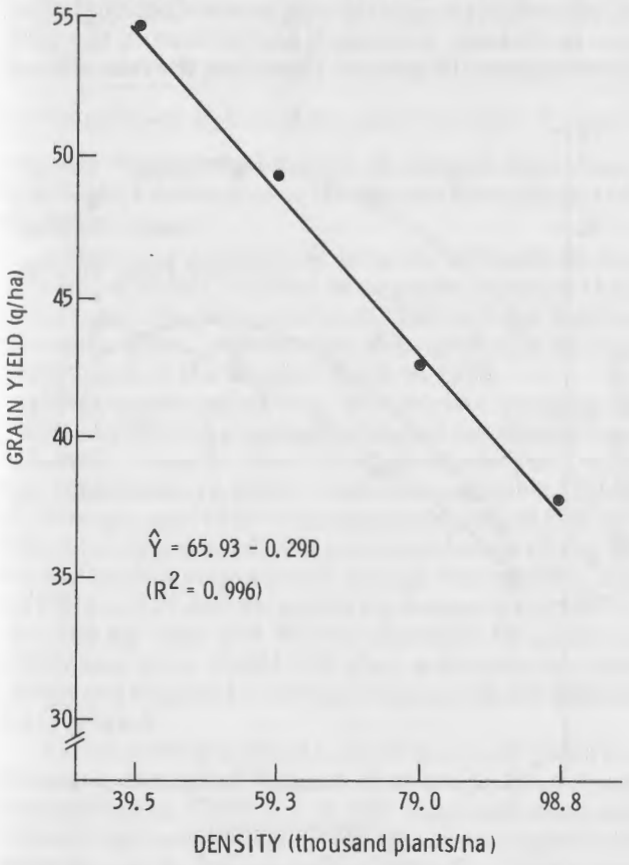

Figure 4. Predicted grain-yield response to plant density for five maize variety hybrids. Plotted points are observed yields.

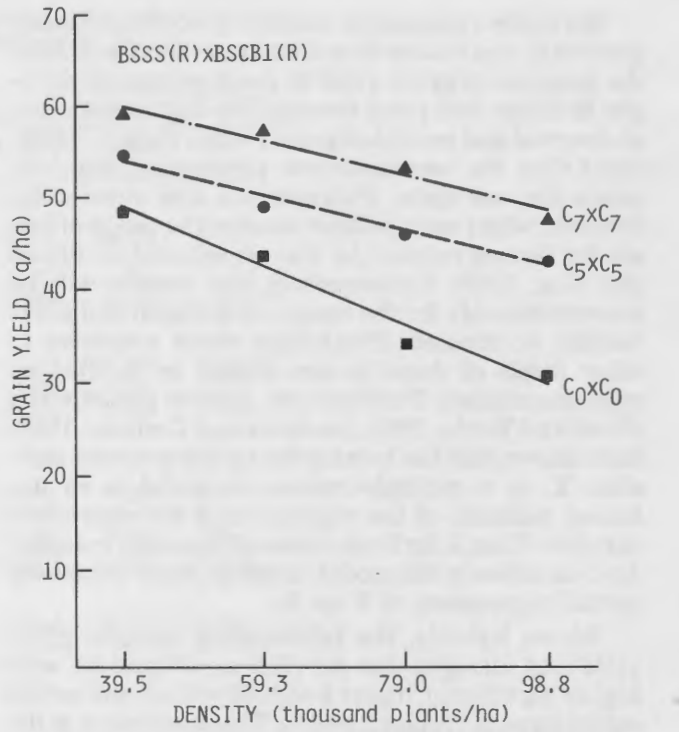

Figure 5. Predicted responses to plant density for variety hybrids of BSSS(R) x BSCB1(R). Plotted points are observed yields.

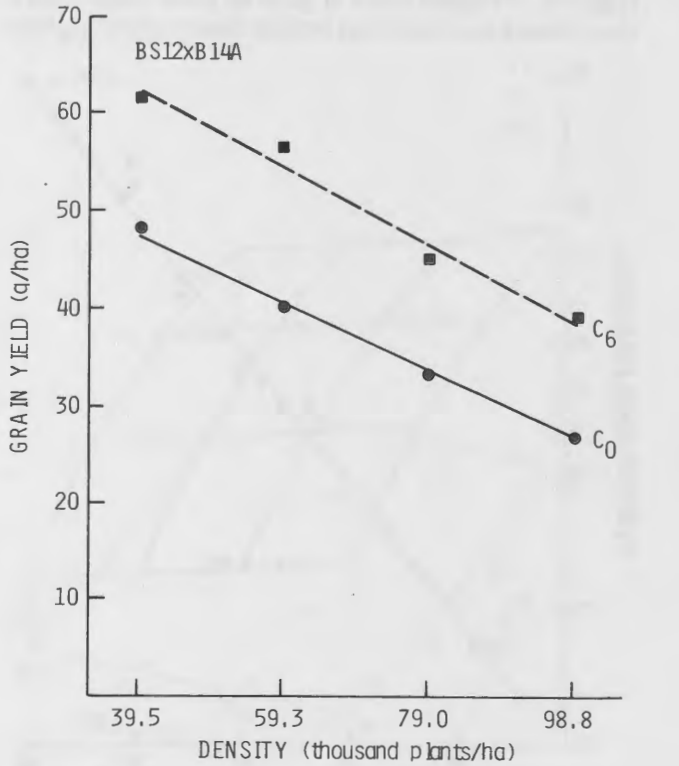

Figure 6. Predicted responses to plant density for variety hybrids of BS12. Plotted points are observed yields.

Multiple-regression models involving linear, quadratic, and interaction terms were used to predict the response of grain yield to combinations of nitrogen fertilizer and plant density. The high correlation of observed and predicted grain yields (Figure 7) indicated that the second-degree polynomial was adequate for our data. Polynomials are unreliable, however, when extrapolated outside the range of levels for factors covered by the experiment (Cochran and Cox, 1957). Consequently, our results will be interpreted only for the ranges of nitrogen and plant density we studied. Predictions about responses to other levels of these factors should be verified by experimentation. Furthermore, several statisticians (Steel and Torrie, 1960; Snedecor and Cochran, 1967) have shown that the b-value for an independent variable, X, in a multiple-regression model is an unbiased estimate of the regression of the dependent variable, Y, on X for fixed values of the other independent variables in the model. In effect, the b-values are partial regressions of Y on X.

Across hybrids, the relationship between grain yield and nitrogen was curvilinear (Figure 8), with highly significant linear b-values within and across environments (Tables 2 and 5). The experiment at the Bruner Farm in 1975 had the highest linear response to nitrogen, probably a consequence of the severe moisture stress that occurred in that environment. Because moisture was limiting, absorption of nitrogen by plants probably was reduced; therefore, each additional unit of nitrogen absorbed by the plant resulted in higher rates of gain in yield. Conversely, the Ankeny environment (which received the highest amount of moisture) had the lowest rate of linear response to nitrogen. Differences between environments for rates of linear response to nitrogen may be attributable to residual levels of nitrogen in each environment. Although residual levels of soil nitrogen were not determined for these environments, comparisons of mean yields at nitrogen levels within environments suggested that levels of residual nitrogen in Ankeny were much higher than in the other environments (Figure 9). Therefore, the rate of linear

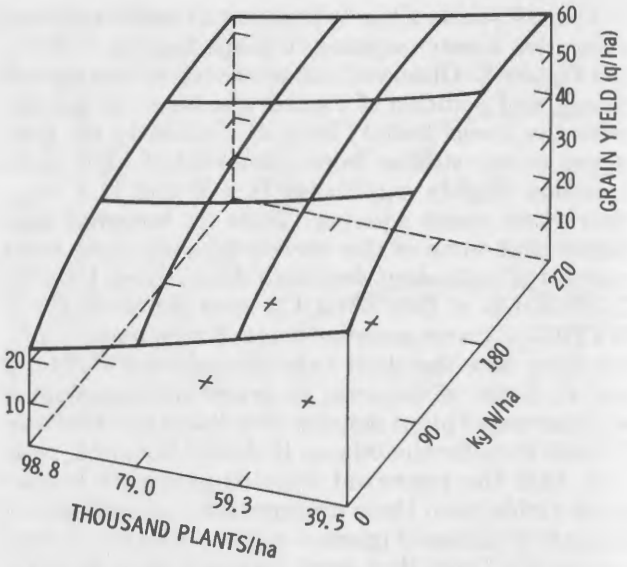

Figure 8. Predicted response surface to combinations of nitrogen and plant density for grain yield of five maize variety hybrids.

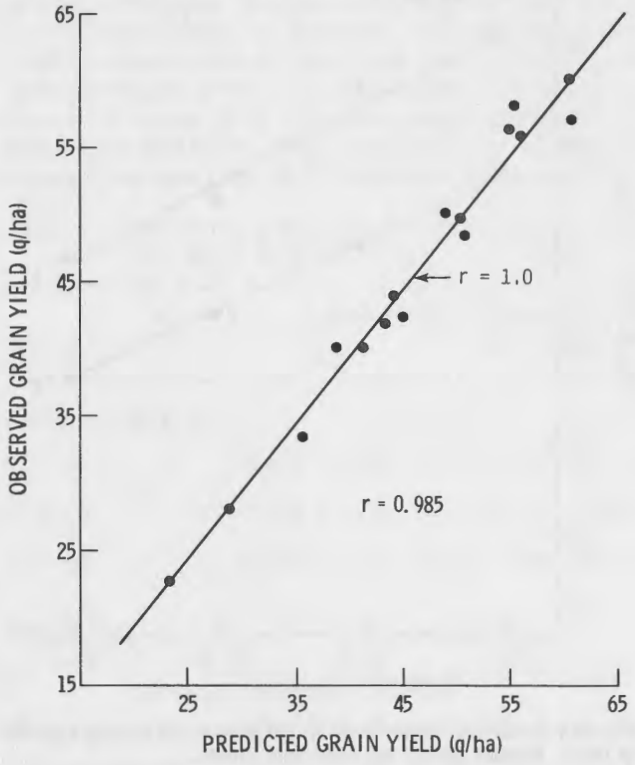

Figure 7. Relationship between observed and predicted grain yields of five maize variety hybrids.

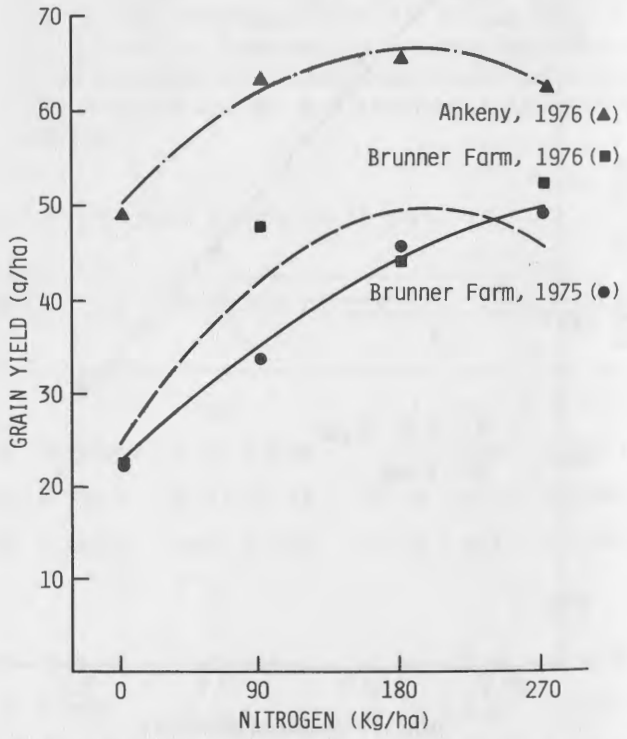

Figure 9. Predicted grain-yield responses to nitrogen fertility in three environments for five maize variety hybrids. Plotted points are observed yields.

Table 5. Multiple regression parameters for the influence of nitrogen (N) and plant density (D) on grain yields of five maize variety hybrids grown in three environments.

	Regression parameters						
	b_0	b_1N	b_2D	$b_3(N^2)$	$b_4(D^2)$	$b_5(ND)$	R^2
Hybrids combined							
Bruner Farm, 1975	39.05	17.002**	-0.282	-2.235	0.001	-0.014	0.922
Bruner Farm, 1976	57.26	24.888**	-0.660	-6.829**	0.002	0.021†	0.873
Ankeny, 1976	68.05	13.279**	-0.065	-4.814**	-0.003	0.062†	0.958
Environments combined	54.79	18.390**	-0.336	-4.626**	0.000	0.023	0.970
BSSS(R)C0 x BSCB1(R)C0							
Bruner Farm, 1975	36.98	19.376**	-0.360	-3.833*	0.001	-0.014	0.830
Bruner Farm, 1976	39.25	27.273**	-0.322	-4.975	0.000	-0.064	0.910
Ankeny, 1976	77.34	11.666**	-0.606	-3.627*	0.001	0.030	0.899
Environments combined	51.19	19.438**	-0.429	-4.145**	0.001	-0.016	0.940
BSSS(R)C5 x BSCB1(R)C5							
Bruner Farm, 1975	51.06	16.506†	-0.683	-2.187	0.004	-0.024	0.759
Bruner Farm, 1976	34.58	27.985**	-0.034	-6.074**	-0.001	-0.059	0.817
Ankeny, 1976	78.16	9.418	-0.450	-3.208*	0.001	0.050	0.774
Environments combined	54.60	17.970**	-0.389	-3.823**	0.002	-0.011	0.924
BSSS(R)C7 x BSCB1(R)C7							
Bruner Farm, 1975	18.12	14.319	0.648	-1.791	-0.007	0.032	0.812
Bruner Farm, 1976	66.64	22.729**	-0.822	-7.181**	0.004	0.074	0.795
Ankeny, 1976	62.75	14.988*	0.259	-6.358**	-0.004	0.070	0.781
Environments combined	49.17	17.345**	0.028	-5.110	-0.002	0.059	0.894
BS12C0 x B14A							
Bruner Farm, 1975	41.43	10.352†	-0.480	-1.194	0.002	0.013	0.883
Bruner Farm, 1976	71.60	20.743	-1.074	-8.615	0.004	0.090	0.782
Ankeny, 1976	75.01	4.721	-0.265	-4.372	-0.003	0.189†	0.729
Environments combined	62.68	11.939*	-0.606	-4.727**	0.001	0.097†	0.900
BS12C6 x B14A							
Bruner Farm, 1975	47.68	24.457**	-0.536	-2.171	0.002	-0.079	0.939
Bruner Farm, 1976	74.24	25.711†	-1.047	-7.297*	0.005	0.063	0.745
Ankeny, 1976	47.00	25.601**	0.739	-6.507**	-0.009*	-0.029	0.938
Environments combined	56.30	25.256**	-0.282	-5.325**	-0.001	-0.015	0.936

†,*,**Significant at 0.10, 0.05, and 0.01 levels of probability, respectively.

response of grain yield to applied nitrogen should not be as high at Ankeny as at the Bruner Farm (Rehm et al., 1976).

Addition of a quadratic term for nitrogen to the regression model resulted in negative b-values that usually were highly significant (Tables 2 and 5). The quadratic term, however, was not significant for the experiment at the Bruner Farm in 1975.

Within nitrogen levels, the relative ranking of yields at different plant densities did not change significantly (Table 5). Also, influence of nitrogen x density interaction on grain yield was negligible (Table 2). Nitrogen and plant-density combinations that resulted in highest predicted grain yield were 270 kg N/ha and 39,500 plants/ha for Bruner Farm, 1975; 180 kg N/ha and 39,500 plants/ha for Bruner Farm, 1976; and 180 kg N/ha and 39,500 plants/ha for Ankeny. Maximum grain yield (61.5 q/ha) across all environments was obtained at 180 kg N/ha and 39,500 plants/ha (Figure 8).

Each hybrid displayed a quadratic grain-yield response to nitrogen (Figures 10 through 14). Across environments, C0 x C0 of the reciprocal program showed higher linear and lower quadratic response to nitrogen than did C7 x C7 (Table 5). Contrarily, BS12C6 x B14A demonstrated a higher linear response to nitrogen than did BS12C0 x B14A. Within

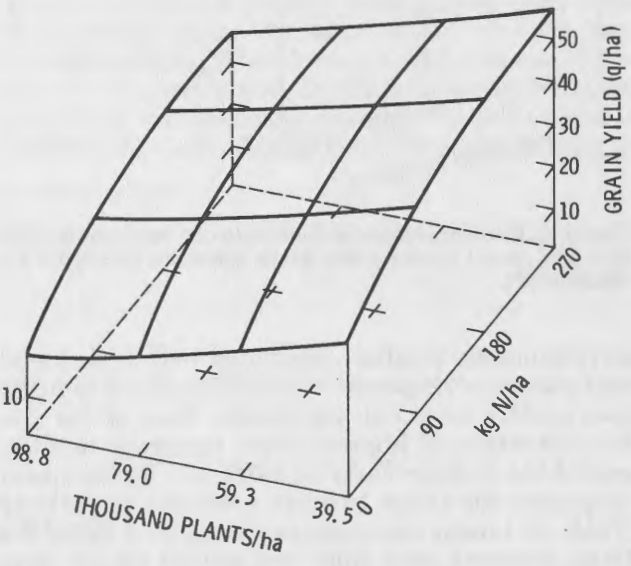

Figure 10. Predicted response surface to combinations of nitrogen and plant density for grain yield of BSSS(R)C0 x BSCB1(R)C0.

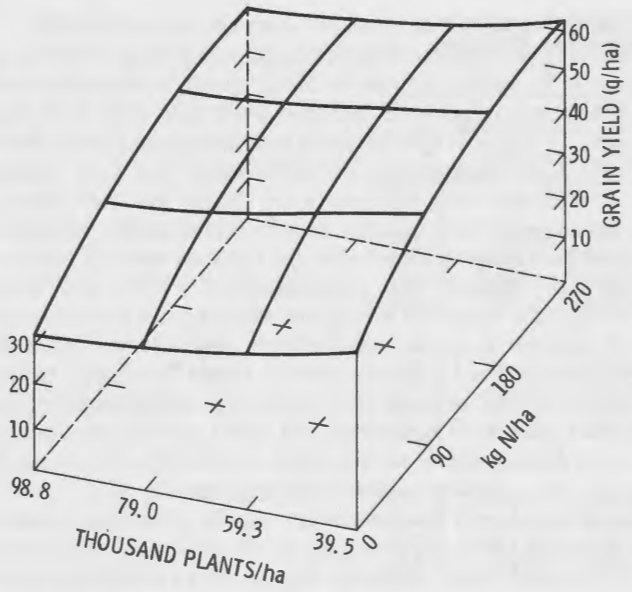

Figure 11. Predicted response surface to combinations of nitrogen and plant density for grain yield of BSSS(R)C5 x BSCB1(R)C5.

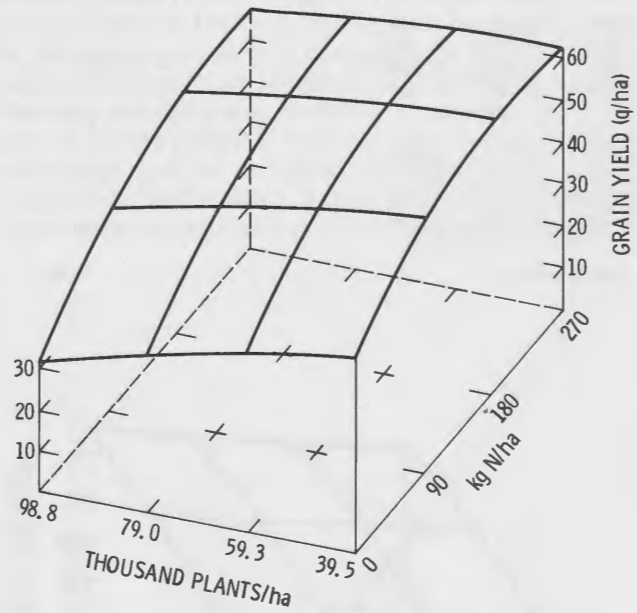

Figure 12. Predicted response surface to combinations of nitrogen and plant density for grain yield of BSSS(R)C7 x BSCB1(R)C7.

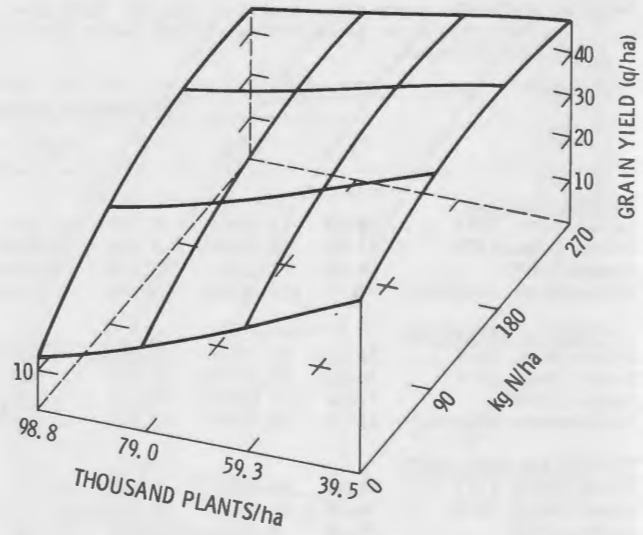

Figure 13. Predicted response surface to combinations of nitrogen and plant density for grain yield of BS12C0 x B14A.

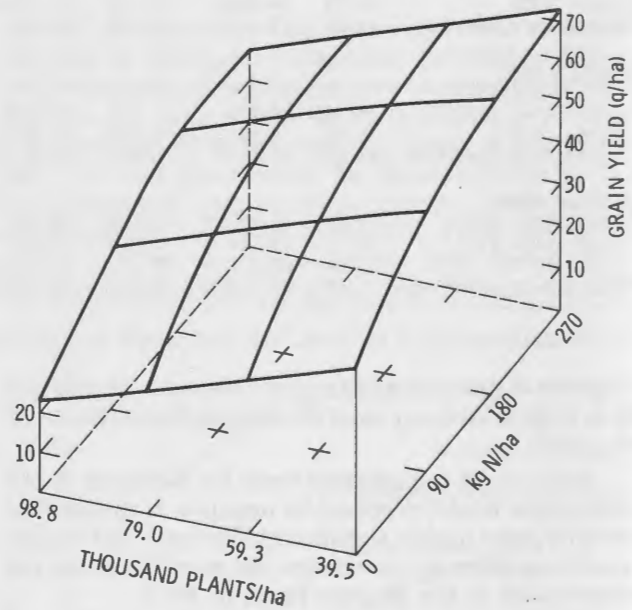

Figure 14. Predicted response surface to combinations of nitrogen and plant density for grain yield of BS12C6 x B14A.

environments, b-values associated with both linear and quadratic responses of BS12C0 x B14A to nitrogen usually were not significant. Four of the five hybrids displayed highest linear responses to nitrogen at the Bruner Farm in 1976, and lowest linear responses for these hybrids occurred at Ankeny (Table 5). Linear responses to nitrogen for BS12C6 x B14A, however, were high and similar for all three environments. Evidently, this variety hybrid possessed the ability to utilize nitrogen efficiently regardless of prevailing environmental conditions. Efficiency of nitrogen utilization by the other four hybrids was influenced by environmental conditions. Increased ability to utilize nitrogen that was associated with recurrent selection for grain yield in BS12 could have been accomplished through an improved root system in the C6 relative to the C0 of this variety. This improved root system would mean that BS12C6 x B14A has the ability to absorb larger amounts of nitrogen than BS12C0 x B14A.

In a diallel cross of four inbred lines of maize (WF9, A257, Oh43, and B14), Powell (1968) found that single-cross hybrids involving B14 outyielded other hybrids at all fertility levels and all environments he studied. Yield advantages for hybrids having B14 as one parent were especially evident at medium (450 kg N, 170 kg P, and 340 kg K per

hectare) and high (1350 kg N, 504 kg P, and 1008 kg K per hectare) fertility levels. Powell's results suggested that inbred B14 was highly responsive to nitrogen. If BS12 *per se* responds poorly to nitrogen and if ability to respond to nitrogen is characterized by additive gene effects, one could hypothesize that major, favorable alleles from B14 (hereafter designated N_r alleles) have selected similar, favorable alleles in BS12 as recurrent selection progressed. Penny et al. (1962) reported that BS12 was highly heterogeneous. Presumably, genotypes that were responsive to high fertility levels were selected and recombined during each cycle of selection in BS12. Consequently, BS12C6 x B14A possessed a higher frequency of N_r alleles than did BS12C0 x B14A. Because BS12C0 possessed a higher frequency of less favorable alleles (hereafter designated n_r alleles) than N_r alleles, it responded poorly to nitrogen. Probably, the slight response of BS12C0 x B14A to nitrogen resulted largely from the additive effect produced by N_r alleles from B14A in combination with the few N_r alleles from BS12C0. In other words, BS12C0 x B14A did not possess the ability to respond to nitrogen because frequency of n_rn_r and N_rn_r was higher than that of N_rN_r. (Note that effects of N_rN_r would be larger than N_rn_r, which, in turn, would be larger than n_rn_r.) Similarly, one could hypothesize that both BSSS and BSCB1 possessed lower frequencies of N_r alleles than n_r alleles. Consequently, the probability of selecting lines with high frequencies of N_r alleles in these populations would be lower than in BS12. Also, because these populations were reciprocal testers, selection of N_r alleles has been at a slow rate. Consequently, efficiency of nitrogen use of BSSS(R)C7 x BSCB1(R)C7 relative to BSSS(R)C0 x BSCB1(R)C0 was similar at all levels of nitrogen evaluated (Table 4).

Generally, the linear term for plant density contributed negatively to grain yield for each hybrid within and across environments (Table 5). The linear and quadratic terms for plant density, and the nitrogen x density interaction term, were not significant and were relatively small compared with the linear and quadratic terms for nitrogen. Also, magnitudes of the b-values associated with the quadratic term for nitrogen, usually, were smaller than the linear b-values. It can be concluded, therefore, that plant density did not influence grain yield of these five variety hybrids as much as did nitrogen, and that the response to nitrogen primarily was linear.

Optimum nitrogen-plant-density combinations for obtaining highest grain yields of the hybrids were 270 kg N/ha and 39,500 plants/ha for BSSS(R)C0 x BSCB1(R)C0, BSSS(R)C5 x BSCB1(R)C5, and BS12C6 x B14A (Figures 10, 11, and 14, respectively) and 180 kg N/ha and 39,500 plants/ha for BSSS(R)C7 x BSCB1(R)C7 and BS12C0 x B14A (Figures 12 and 13, respectively). Evidently, application of high rates of nitrogen did not improve the ability of these hybrids to tolerate high plant densities.

Grain-yield components

Number of ears per 100 plants increased as recurrent selection for grain yield progressed in both programs (Table 6). Eberhart et al. (1973) and Russell et al. (1973) reported similar results after five cycles of reciprocal recurrent selection and half-sib selection, respectively. Several other researchers (Moll and Stuber, 1971; Horner et al., 1976; Allan and Darrah, 1978; Darrah et al., 1978) have reported consistent, positive correlations between ear number and grain yield in other recurrent selection programs. Also, results of studies by Collins et al. (1965) and Russell (1968) showed that increased ear productivity at high plant densities (i.e., reduced barrenness) accounted for the grain-yield advantages of prolific over nonprolific maize genotypes.

Relative ranking of the genotypes for ear productivity was consistent across evaluation environments and levels of nitrogen; i.e., interactions of genotypes with environments and nitrogen were not significant. Although the improved hybrids demonstrated greater abilities to produce more ears at high plant densities (Figure 15), none of the hybrids was strongly prolific. Therefore, possibly because of genetic or environmental limitations, improvement of prolificacy via recurrent selection for grain yield in BSSS(R), BSCB1, and BS12 did not occur. Lonnquist

Table 6. Grain-yield components and flowering traits of five maize variety hybrids.

	No. ears/ 100 plants	Grain/ plant (g)	Ear length (cm)	Ear diameter (cm)	Cob diameter (cm)	Kernel depth (cm)	Kernel row no.	Kernel wt. (g/300 kernels)	Kernel moisture (%)	Pollen shed (Days from July 1)	Silk emergence	Pollen-shed-to-silking interval
BSSS(R) x BSCB1(R)												
C0 x C0	70.0	74.2	15.3	4.2	2.4	0.90	16.1	67.1	22.9	26.4	33.0	6.5
C5 x C5	81.1	87.5	16.3	4.3	2.5	0.85	16.7	67.9	22.3	27.5	32.5	5.0
C7 x C7	83.6	99.4	16.1	4.3	2.4	0.92	16.7	71.2	24.6	27.8	33.0	4.9
BS12 x B14A												
C0	65.2	72.0	17.8	4.2	2.4	0.89	15.5	81.5	18.9	26.4	34.3	7.9
C6	75.0	94.7	18.1	4.3	2.5	0.90	16.0	82.5	21.6	26.8	31.7	4.9
$LSD_{.05}$	3.2	4.8	0.4	0.1	0.1	0.02	0.3	1.4	0.8	0.5	0.9	0.5

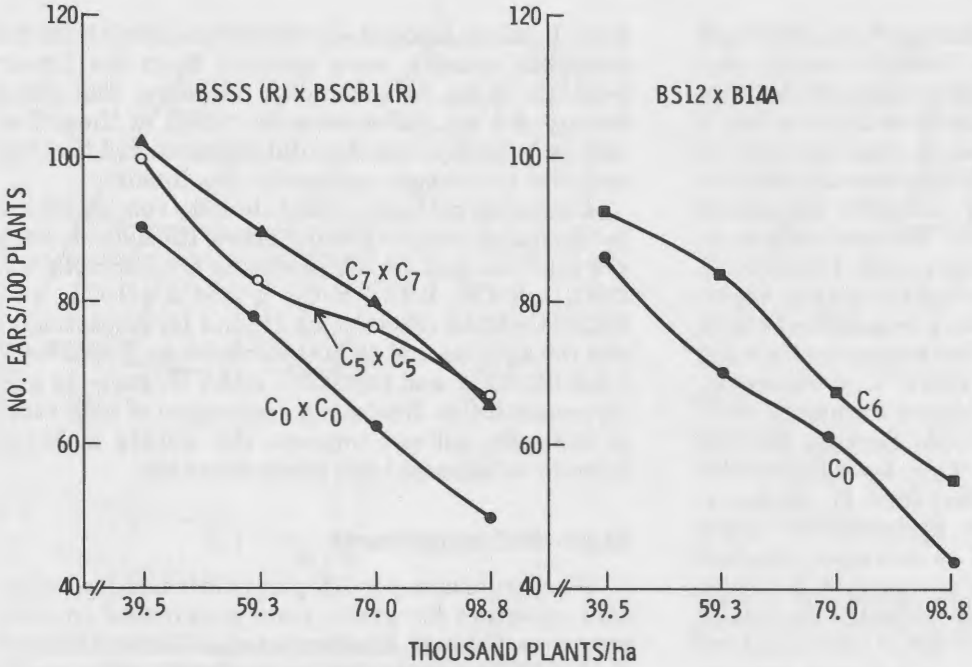

Figure 15. Effect of plant density on number of ears per 100 plants of five maize variety hybrids.

(1967), however, observed significant improvement in grain yield via mass selection for prolificacy. If most Iowa maize populations are similar to those evaluated by Lonnquist, the ideotype proposed for central Iowa (Mock and Pearce, 1975) would have to be developed by deliberate selection for prolific, high-yielding genotypes.

Definite trends for increased grain yield per plant were observed (Table 6) although selection was based on grain yield per unit land area in these programs. Also, kernel weight increased significantly with selection in the reciprocal recurrent selection program, but not in the half-sib program (Table 6). Probably, increased grain per plant of BSSS(R)C7 x BSCB1(R)C7 relative to its counterparts resulted from increased ear number and kernel weight. Increased grain yield per plant of BS12C6 x B14A relative to BS12C0 x B14A could not be explained on the basis of kernel weight, but by various other yield components (Table 6.)

Overall, kernel weight was not affected by nitrogen. Furthermore, genotype x nitrogen, genotype x density, and all higher-order interactions involving genotypes, nitrogen, and density were not significant for this trait. These observations, coupled with the nonsignificant differences between BS12C0 x B14A and BS12C6 x B14A for kernel weight, suggest:(1) kernel weight had reached its optimum genetic potential and could not be influenced by controllable environmental factors (i.e., nitrogen and plant density), (2) rates of nitrogen and plant density we used were not of sufficient magnitudes to exert noticeable influences on the expression of kernel weight, and (3) either the source (i.e., the photosynthetic potential) or the sink (i.e., capacity of grain to store photosynthate) was limiting kernel weight. Thorough explanations for these possibilities are beyond the scope of our studies. After examining the data obtained for leaf-area estimates, however, we will discuss the model that best explains our results.

Although usually significant statistically, increases in ear length, ear diameter, cob diameter, kernel depth, and kernel row number associated with selection for grain yield were small (Table 6). Statistically significant correlations between grain yield and ear and kernel traits often have been observed in maize (Obilana and Hallauer, 1974; Crosbie et al., 1978). The proportion of grain-yield variation attributable to these traits, however, is usually small and is highly influenced by genotype x environment interactions (Obilana and Hallauer, 1974). In our studies, several interactions of genotype with environment and with specific environmental factors were observed for ear length, kernel row number, and kernel depth. Probably, ear and kernel traits *per se* would be inadequate indexes for indirect selection for grain yield in maize.

Data obtained for kernel moisture at harvest (Table 7) indicated that plots to which nitrogen fertilizer was applied matured earlier than those that re-

Table 7. Influence of rates of nitrogen on percent kernel moisture at harvest for five maize variety hybrids.

Hybrid	kg N/ha†			
	0	90	180	270
BSSS(R) x BSCB1(R)				
C0 x C0	24.0	22.9	22.1	22.7
C5 x C5	25.8	21.8	20.4	21.4
C7 x C7	27.8	23.9	22.8	23.7
BS12 x B14A				
C0	20.1	19.0	17.9	18.5
C6	24.5	21.3	20.0	20.7
$\bar{X}_{nitrogen}$	24.4	21.8	20.6	21.4

†$LSD_{.05}$ for nitrogen = 1.24, and for hybrid x nitrogen = 1.52.

ceived no nitrogen treatment. Contrarily (as indicated by nonsignificant mean squares for density and all interactions with density), plant density had no effect on kernel moisture. Maturities of BSSS(R)C0 x BSCB1(R)C0 and BSSS(R)C5 x BSCB1(R)C5 were similar, but BSSS(R)C7 x BSCB1(R)C7 was considerably later maturing than both (Table 6). Differences in kernel moisture between BSSS(R)C0 x BSCB1(R)C0 and BSSS(R)C7 x BSCB1(R)C7, however, were not significant for the plots that received nitrogen (Table 7). BS12C6 x B14A matured later than BS12C0 x B14A, and this difference occurred at all nitrogen levels.

Flowering dates

Number of days to 50% pollen shed (DPS) and 50% silk extrusion (DSE), and pollen-shed-to-silking interval (PSSI), decreased as nitrogen rates increased (Figure 16). Usually, 180 kg N/ha was optimum for early pollen shed, early silk extrusion, and reduced PSSI.

Delayed 50% pollen shed and 50% silk emergence were associated with increased plant density (Figure 17); consequently, PSSI increased as plant density increased. These findings agree with previous reports (Woolley et al., 1962; Pepper, 1974; Fakorede, 1975; Fakorede and Mock, 1978a).

Significant changes in DPS, DSE, and PSSI were associated with recurrent selection for grain yield in both BSSS(R) x BSCB1(R) and BS12 x B14A (Table 6). BSSS(R)C7 x BSCB1(R)C7attained 50% pollen shed later than BSSS(R)C0 x BSCB1(R)C0; both hybrids, however, displayed incipient silks on approximately the same day. Consequently, PSSI of BSSS(R)C7 x BSCB1(R)C7 was shorter than that of its unimproved counterpart. Also, both genotypes from the half-sib program reached 50% pollen shed on approximately the same day, but BS12C6 x B14A reached DSE earlier than BS12C0 x B14A. Therefore, PSSI for BS12C6 x B14A was 3 days shorter than that of BS12C0 x B14A. We obtained similar results for these hybrids in another study (Fakorede and Mock, 1978a).

Pollen-shed-to-silking interval is a useful indicator of density stress in maize. Genotypes that are tolerant of high density stress usually display a shorter interval between 50% pollen shed and 50% silk emergence than intolerant genotypes when grown under high plant densities (Mock and Buren, 1972; Buren et al., 1974; Mock and Pearce, 1975). The data we obtained for grain yield and PSSI agree with those reported by Buren et al. (1974); i.e., a negative association exists between the two traits. Because selection for grain yield resulted in decreased PSSI, one could propose a common biochemical pathway as the genetic mechanism underlying the association between pollen shed and silk emergence in maize. There are, however, modifier genes that affect either one or both of the traits; consequently, variation is observed among maize genotypes for PSSI. Several researchers (Grogan, 1956; Duvick, 1958; Chinwuba et al., 1961; Schwanke, 1965; Meyer, 1970) have shown that detasseled or male-sterile maize genotypes were 5 to 55% higher yielding than their male-fertile counterparts, and these yield advantages were especially evident at high plant densities. Usually, male-sterile hybrids silked earlier and displayed reduced silking interval (usually, number of days between incipient silk extrusion and 75 or 80% silk extrusion by plants in a plot) than hybrids having normal cytoplasms. Noble and Russell (1963) reported significant decreases in PSSI for certain natural restorer lines when tested in male-sterile cytoplasms. These results suggest that pollen shed, silk emergence, and grain yield are closely related during the ontogeny of maize plants.

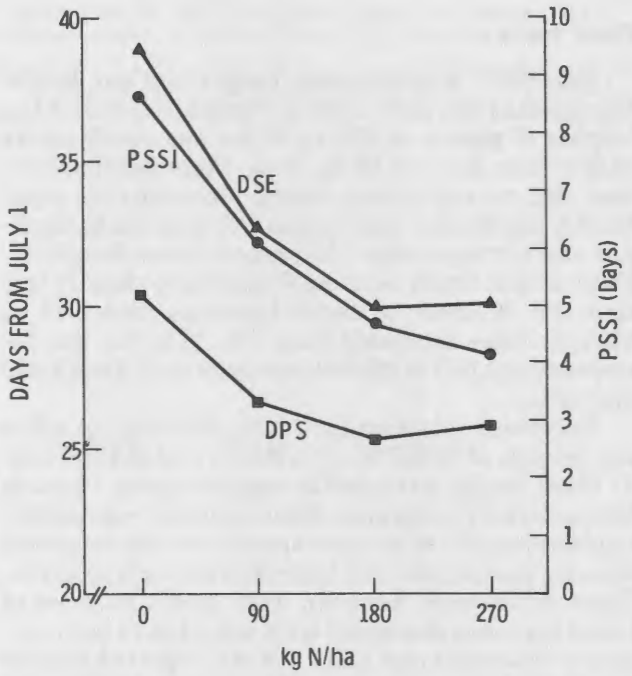

Figure 16. Effect of nitrogen on flowering dates of five maize variety hybrids.

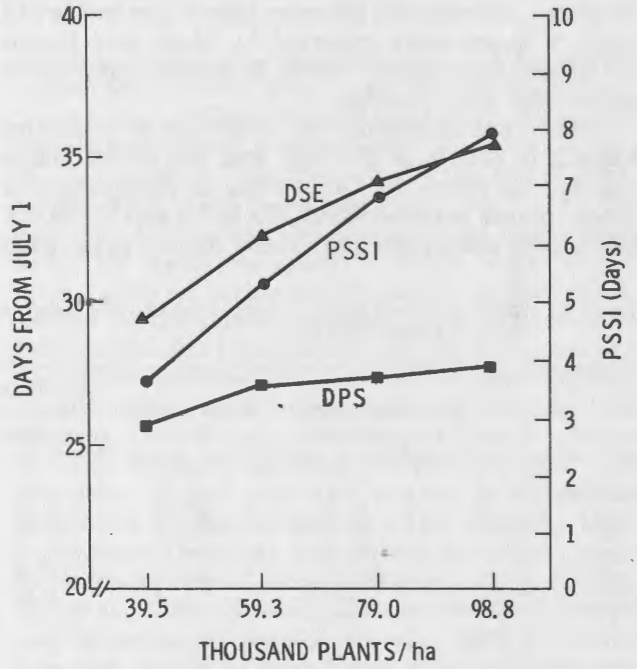

Figure 17. Effect of plant density on flowering dates of five maize variety hybrids.

Plant traits

Generally, mature plant height and ear height increased as nitrogen rates increased (Table 8). Also, lodging of plants at 270 kg N/ha was significantly higher than at 0 and 90 kg N/ha. Plant density, however, had no significant effects on means for plant height, ear height, and lodging. Across plant densities and nitrogen rates, differences in ear-height-to-plant-height ratios were small and were slightly less than 0.5. Number of tassel branches increased as nitrogen rates increased from 0 to 90 kg/ha, but decreased from 18.3 at 39,500 plants/ha to 16.3 at 79,000 plants/ha.

Recurrent selection for grain yield did not affect ear heights of BSSS(R), BSCB1(R), and BS12 (Table 8). Plant height increased by approximately 10 cm in both selection programs. Consequently, ear-height-to-plant-height ratios were smaller for the improved than for the unimproved hybrids from each program. These differences, however, were small. Number of tassel branches decreased with selection in both programs. Fakorede and Mock (1978a) reported similar results for these same genotypes in other studies and also found that tassel weight decreased considerably for the improved relative to the unimproved hybrids. Negative associations between tassel size and grain yield of maize were reported by Mock and Buren (1972) and Buren et al. (1974). Results of our studies agree with their results.

Recurrent selection was effective in reducing lodging of plants of BSSS(R) and BSCB1(R) maize populations (Table 8). Differences in percentages of lodged plants between BS12C0 x B14A and BS12C6 x B14A were not significant. These results agree with data reported earlier (Fakorede and Mock, 1978b), which showed that selection for stalk quality (i.e., rind puncture and stalk-breaking force) was successful in BSSS(R) and BSCB1(R) but not in BS12.

Leaf area

Application of 90 kg N/ha increased the number of leaves per plant from 9.9 to 11.2 (Table 9). Furthermore, ear-leaf area increased as the nitrogen rate increased from 0 to 180 kg/ha, indicating that 180 kg N/ha was optimum for leaf area per plant and leaf-area index. The traits, grain yield (Figure 1), leaf area, and leaf-area index (Table 9), therefore, demonstrated similar responses to nitrogen.

Number of leaves per plant and ear-leaf area decreased as plant density increased (Table 9). Leaf area per plant also decreased from 0.70 m^2 at 39,500 plants/ha to 0.59 m^2 at 98,800 plants/ha. These results agree with earlier reports (Earley, 1965; Nunez and Kamprath, 1969; Pepper, 1974; Fakorede, 1975; Fakorede et al., 1977; Fakorede and Mock, 1978a) and suggest that this decrease was a consequence of greater interplant competition at high rather than at low plant densities. Conversely, leaf-area index increased significantly as plant density was increased from 39,500 to 98,800 plants/ha (Table 9). This, too, has been reported previously (Nunez and Kamprath, 1969; Pepper, 1974; Fakorede, 1975; Fakorede and Mock, 1978a).

Similar to the results obtained by Nunez and Kamprath (1969), efficiency of leaf area for producing grain increased as nitrogen rate increased from 0 to 90 kg/ha (Table 9), but this efficiency was not increased further at higher levels of nitrogen. Grain per

Table 8. Effects of nitrogen, plant density, and genotype on plant traits of five maize variety hybrids.

	Ear height (cm)	Plant height (cm)	Ear height: plant height ratio	Tassel branch no.	% lodging
kg N/ha					
0	81.4	183.9	0.44	14.0	17.8
90	99.0	212.9	0.46	17.4	16.3
180	106.7	219.0	0.49	18.4	23.8
270	113.2	229.6	0.49	18.1	26.1
$LSD_{.05}$	11.0	6.8	0.04	1.6	7.5
Plants/ha					
39,500	98.7	211.6	0.47	18.3	18.8
59,300	100.1	212.5	0.47	17.2	21.8
79,000	102.3	213.1	0.48	16.3	20.6
98,800	99.3	208.1	0.48	16.0	22.9
$LSD_{.05}$	NS	NS	0.01	1.4	NS
BSSS(R) x BSCB1(R)					
C0 x C0	98.9	204.0	0.48	20.9	27.5
C5 x C5	100.5	208.3	0.48	18.7	24.6
C7 x C7	99.6	214.3	0.46	16.5	17.3
BS12 x B14A					
C0	100.4	210.0	0.48	15.8	19.0
C6	101.0	220.1	0.46	12.9	16.8
$LSD_{.05}$	NS	3.3	0.01	1.0	3.6

Table 9. Effects of nitrogen, plant density, and genotype on number of leaves, leaf area, and leaf-area-derived traits of five maize variety hybrids.

	No. leaves/plant	Ear leaf area (cm^2)	Plant leaf area (m^2)	Leaf area index	Grain/leaf area (mg/cm^2)
kg N/ha					
0	9.9	566.7	0.53	3.4	7.9
90	11.2	655.2	0.62	3.9	11.8
180	12.0	747.2	0.70	4.5	11.6
270	12.4	754.1	0.71	4.5	12.7
$LSD_{.05}$	1.0	44.0	0.04	0.3	2.2
Plants/ha					
39,500	12.4	749.3	0.70	2.6	18.8
59,300	11.5	690.1	0.65	3.6	11.4
79,000	10.9	655.8	0.62	4.6	8.0
98,800	10.7	628.0	0.59	5.4	5.9
$LSD_{.05}$	0.4	24.3	0.02	0.2	0.7
BSSS(R) x BSCB1(R)					
C0 x C0	11.0	641.6	0.60	3.8	10.2
C5 x C5	11.2	659.2	0.62	4.0	11.8
C7 x C7	11.4	706.5	0.66	4.2	12.6
BS12 x B14A					
C0	11.3	686.4	0.64	4.1	8.6
C6	11.8	710.2	0.67	4.3	11.8
$LSD_{.05}$	0.3	20.5	0.02	0.2	0.8

unit leaf area decreased significantly with increased plant density. Evidently, leaf area per plant and production of grain per unit leaf area were more important in determining grain yield at high plant densities than was leaf-area index *per se*.

Number of leaves per plant of the improved hybrids was slightly greater than that of the unimproved hybrids (Table 9). These differences were significant statistically because of the low coefficient of variation (C.V. = 6.84%) associated with this trait; a consequence of small error mean square (0.604) and a high overall mean for the trait (11.4).

Improved hybrids produced larger ear leaves, larger leaves per plant, and larger leaf-area indexes than the unimproved hybrids (Table 9). Theoretically, gross production of photosynthate should have been higher in the improved than in the unimproved hybrids. Data obtained for grain yield (Table 1) and grain-yield components (Table 6) implied that improved hybrids produced and translocated more photosynthate into the ear than did unimproved hybrids. Additionally, genotypic differences for grain per unit leaf area (Table 9) suggested that the improved hybrids were more efficient in production of photosynthate than were the unimproved hybrids. Evidently, improvements in grain yield and grain-yield components associated with recurrent selection in BSSS(R) x BSCB1(R) and BS12 resulted from increased gross photosynthesis and efficient production of grain per unit leaf area.

Our results demonstrated that increased rates of nitrogen did not increase kernel weight and that differences for kernel weight between BS12C0 x B14A and BS12C6 x B14A were not significant. Murata (1968) divided the process of yield production in grain crops into three stages: (1) formation of organs for nutrient absorption and photosynthesis, (2) formation of flower organs and "yield containers," and (3) production, accumulation, and translocation of "yield contents" (photosynthate). For maize, capacity for grain yield can be expressed as: Yield = (No. ears/unit land area) (No. kernels/ear) (weight/kernel). The "yield containers" (or the sinks) depend upon supply of assimilates from the photosynthetic system (or the source) to attain their maximum genetic potentials. Physical capacity for storage of photosynthate, however, is determined by environmental conditions that occur before flowering (Murata, 1968; Hanway, 1971; Evans, 1974). Application of nitrogen in early stages of seedling growth promotes rapid expansion of leaf area and usually is effective in increasing dry-matter accumulation (Murata, 1968).

Increased nitrogen supply may not always result in increased rate of photosynthetic activity per unit leaf area, although total photosynthesis of the crop may be enhanced greatly (Murata, 1968). If the sink size and ability to translocate photosynthate from source to sink are not limiting, increased grain yield should occur with increased total photosynthesis of individual plants. Evidently, total photosynthesis increased (as a result of increased leaf area) with increased nitrogen rates from 0 to 180 kg/ha and also for the improved relative to the unimproved hybids (Table 9). Increased grain yield associated with increased nitrogen from 0 to 180 kg/ha (Figure 1) and with improved hybrids (Table 1) indicated that translocation of photosynthate from source to sink was not limiting for the genotypes in our study. The increased photosynthate, however, was utilized primarily in the formation and filling of grains on more ears (Table 6).

As indicated by small, but significant, increases in ear length, number of kernel rows, and ear diameter, some of the increased photosynthate probably was utilized also to increase number of kernels. Kernel weight remained unchanged. Thus, increased grain yield associated with recurrent selection and with increased rates of nitrogen resulted primarily from increased ear productivity per unit land area.

Leaf orientation

Angles of leaves above (AANG) and below (BANG) top ears were not affected by nitrogen fertilizer (Table 10). Lengths of leaves from the point of attachment to the stalk to "flagging" points and total leaf lengths increased with increased nitrogen for both upper (AL_{fp}) and lower (BL_{fp}) canopies. Differences between 180 and 270 kg N/ha for the two traits, however, were not significant. Furthermore, leaf orientation value below the ear (BLOV) was not influenced by fertilizer nitrogen, but 180 and 270 kg N/ha stimulated the development of larger leaf orientation values for the upper canopy (ALOV) than 0 kg N/ha. Therefore, orientation of upper canopies of maize genotypes we studied was more upright at high than at low nitrogen levels.

Our results indicated that, regardless of plant density, AANG, AL_{fp}, ALOV, BL_{fp}, and total lengths of leaves below top ears (BL_T) remained unchanged (Table 10). Total lengths of leaves above top ears (AL_T) decreased slightly (though significantly) at densities higher than 59,300 plants/ha, and BANG increased from 60.1° at 39,500 plants/ha to 63.0° at 98,800 plants/ha. Differences for BANG among 59,300, 79,000, and 98,800 plants/ha were not significant statistically. Usually, BLOV increased with increased plant density. At the high plant densities, therefore, canopy layers below the ears were more upright than they were at the low density. Probably, this resulted from mutual support of plants due to their close proximity at the high plant densities. In another study, Fakorede and Mock (1976) observed no significant differences for ALOV among plant densities, but BLOV increased significantly with increased plant density.

The traits, AANG, AL_{fp}, AL_T, and ALOV of BSSS(R)C7 x BSCB1(R)C7 were significantly greater than those of BSSS (R)C0 x BSCB1(R)C0 (Table 10). Reciprocal recurrent selection for grain yield, therefore, resulted in more upright orientation of upper canopies of the population cross of BSSS(R) and BSCB1(R). Similar results were observed for the lower canopy. The half-sib program was not effective in changing canopy orientation of BS12. Although AANG of BS12 increased significantly from C0 to C6, AL_{fp}, AL_T, and ALOV did not change significantly. Also, BANG of BS12C0 x B14A and BS12C6 x B14A were identical. Lower leaves of BS12C6 x B14A, however, "flagged" less and were longer than those of BS12C0 x B14A. Consequently, BLOV for BS12C6 x B14A was larger than that for BS12C0 x B14A, indicating that lower canopies of BS12C6 x B14A were more upright than those of BS12C0 x B14A. Similar results were observed in other studies conducted with

Table 10. Effects of nitrogen, plant density, and genotype on leaf-orientation values for canopies of five maize variety hybrids.

	Upper canopy				Lower canopy			
	AANG†	AL_{fp} (cm)	AL_T (cm)	ALOV	BANG†	BL_{fp} (cm)	BL_T (cm)	BLOV
kg N/ha								
0	59.1	36.7	74.4	29.5	62.7	45.6	81.0	35.7
90	59.7	45.8	82.4	33.3	61.9	52.9	87.7	37.5
180	60.5	49.4	87.4	34.6	62.5	56.3	93.3	38.1
270	60.7	51.8	88.4	36.0	61.6	58.9	93.7	38.9
$LSD_{.05}$	NS	4.6	5.4	4.3	NS	5.9	4.8	NS
Plants/ha								
39,500	59.2	46.9	84.7	33.1	60.1	51.8	88.8	35.3
59,300	60.1	45.8	84.6	32.8	62.3	53.7	89.5	37.4
79,000	60.6	45.0	82.2	33.4	63.3	52.8	88.9	37.8
98,800	60.1	46.0	81.1	34.2	63.0	55.4	88.5	39.6
$LSD_{.05}$	NS	NS	2.0	NS	1.5	NS	NS	2.2
BSSS(R) x BSCB1(R)								
C0 x C0	58.4	44.8	79.9	32.8	60.4	52.9	87.2	36.8
C5 x C5	62.4	47.6	78.6	37.7	63.8	55.3	84.4	41.7
C7 x C7	61.7	47.8	82.4	35.8	63.6	54.5	88.4	39.1
BS12 x B14A								
C0	57.9	44.1	87.1	29.5	61.4	50.5	91.5	34.1
C6	59.6	45.5	87.8	31.0	61.7	54.0	93.2	40.0
$LSD_{.05}$	1.3	2.2	1.6	1.9	1.4	2.2	1.6	1.9

†Degrees from horizontal.

the improved and unimproved hybrids from these selection programs (Fakorede and Mock, 1978a).

Generally, differences in leaf orientation values for the improved and the unimproved hybrids were too small to be of practical importance. Furthermore, these small differences were consistent (i.e., genotype x density, genotype x nitrogen, and genotype x nitrogen x density mean squares were not significant). Probably, mutual shading at high plant densities was similar for both improved and unimproved hybrids. Mock and Pearce (1975) hypothesized that a maize ideotype adapted to high plant densities should possess smaller, narrower, more erect leaves than those of contemporary maize genotypes. Also, several researchers (Pendleton et al., 1968; Winter and Ohlrogge, 1973; Pepper, 1974; Fakorede and Mock, 1976) indicated that maize genotypes possessing erect leaf orientations were more efficient in converting solar energy into grain than were genotypes with horizontal leaf orientations. These differences were more pronounced at high than at low plant densities. Results from all these studies seem to justify initiation of breeding programs for upright-leaved, density-tolerant, high-yielding maize genotypes.

Dry-matter productivity and harvest index

Dry-matter productivity of the maize genotypes in our studies was affected significantly by nitrogen (Table 11). Dry matter per plant and total dry matter per hectare increased as nitrogen rate was increased from 0 to 90 kg/ha. Also, the difference between 90 and 270 kg N/ha was significant for total dry matter. Differences between 90 and 180 kg N/ha were not significant. Additionally, production of dry matter per unit leaf area increased with nitrogen application, but differences among 90, 180, and 270 kg N/ha were not significant statistically. Probably, rates of photosynthetic activity per unit leaf area of maize genotypes in our studies were similar for rates of nitrogen higher than 90 kg/ha. Presumably, increased grain yield associated with increased application of nitrogen (Figure 1) resulted from increased canopy photosynthesis (Table 9). Research with rice (*Oryza sativa* L.) led to similar conclusions (Murata, 1968).

Although dry matter per unit leaf area and dry matter per plant decreased markedly as plant density increased, dry matter per hectare did not change significantly across plant densities (Table 11). Number of leaves per plant and leaf area per plant were affected significantly by increased plant density (Table 9). Because leaf-area index increased as plant density increased, it can be suggested that decreased leaf area per plant and associated decreased total plant photosynthesis that resulted from increased plant density were counterbalanced by increased leaf-area index. Therefore, dry matter per hectare was not affected significantly by increased plant density.

Harvest index at 0 kg N/ha was significantly lower than it was at the three higher nitrogen rates (Table 11). Differences for this trait among 90, 180, and 270 kg N/ha were not significant. Harvest index decreased with increased plant density. Similarly, total grain yield decreased with increased plant density (Figure 4), but total dry matter remained constant across plant densities (Table 11). Thus, a large biolog-

Table 11. Effects of nitrogen, plant density, and genotype on dry-matter productivity and harvest indices of five maize variety hybrids.

	Total dry matter (t/ha)	Dry matter/plant (g)	Dry matter/ leaf area (mg/cm^2)	Harvest index (%)
kg N/ha				
0	9.2	159.5	29.0	26.8
90	13.6	229.8	36.9	31.9
180	14.4	248.8	35.1	33.5
270	15.9	247.8	38.2	33.3
$LSD_{.05}$	2.3	32.9	5.1	5.1
Plants/ha				
39,500	12.6	340.8	48.1	40.1
59,300	13.6	243.4	37.2	31.4
79,000	13.3	179.2	29.0	29.3
98,800	13.7	149.4	25.1	24.6
$LSD_{.05}$	NS	20.7	2.9	2.2
BSSS(R) x BSCB1(R)				
C0 x C0	12.1	209.1	33.9	29.7
C5 x C5	13.4	229.7	36.2	32.9
C7 x C7	14.2	242.8	35.8	35.0
BS12 x B14A				
C0	12.4	213.8	32.4	26.1
C6	14.4	245.7	35.9	33.2
$LSD_{.05}$	1.0	16.2	2.3	3.1

ical yield does not necessarily signify a large economic yield. Furthermore, Shibles and Weber (1966) demonstrated for soybeans that, because of greater interplant competition, more photosynthate is used for vegetative growth at high than at low plant densities. High plant densities, therefore, result in longer periods of vegetative growth, and there is competition between vegetative and reproductive organs for available photosynthate. Our results agree with this hypothesis.

Clearly, the improved hybrids in our studies were superior to the unimproved hybrids in production of dry matter (Table 11). Relative to the unimproved hybrids, dry matter per plant and total dry matter were significantly higher for the improved hybrids. Also, grain per unit leaf area (Table 9) and harvest index (Table 11) were greater for the improved hybrids. Yield increases associated with recurrent selection in BSSS(R) x BSCB1(R) and BS12, therefore, resulted from increased gross photosynthesis, increased production of photosynthate, and increased translocation of photosynthate from source to sink in the improved populations.

General Discussion and Conclusions

Significant yield improvements in the variety hybrids resulted from reciprocal recurrent selection in BSSS and BSCB1 and half-sib selection in BS12 maize populations. Progress from recurrent selection usually is evaluated in several environments. We observed that rates of gain in grain yield varied widely across rates of nitrogen fertilizer and plant density, suggesting that one should use several levels of these factors in evaluating environments for recurrent selection.

Improved hybrids demonstrated abilities to produce more grain than their unimproved counterparts at all levels of nitrogen fertilizer and plant densities we investigated. All hybrids, however, demonstrated positive curvilinear responses to nitrogen and negative linear responses to plant density. Although the hybrids were intolerant of high plant densities, the negative linear b-values observed for C5 x C5 and C7 x C7 of BSSS(R) and BSCB1(R) were lower than those obtained for the other hybrids, indicating that these two hybrids were more tolerant of high plant densities. Multiple-regression models involving linear, quadratic, and interaction terms were used to predict the optimum combination of nitrogen and plant density for maximum yield of each hybrid across and within environments. Optimum density was 39,500 plants/ha, but optimum nitrogen fertilizer within this density varied among hybrids. Usually, the improved hybrids performed best at 180 or 270 kg N/ha, and the unimproved hybrids were best at 90 or 180 kg N/ha. Regression coefficients for both linear and quadratic terms for plant density and the nitrogen x density interaction term were small and not significant. Contrarily, b-values for nitrogen terms were large and significant, although those for the quadratic term were smaller than for the linear term. We concluded that hybrids in our study primarily displayed linear grain-yield response to nitrogen fertilizer and that the influence of plant density on grain yield was not as important as the influence of nitrogen fertilizer.

In a separate study (Fakorede and Mock, 1978c), we investigated yield stability and adaptation responses of the five variety hybrids evaluated in this study. BSSS(R)C7 x BSCB1(R)C7 and BS12C6 x B14A consistently demonstrated greater adaptation to high-nitrogen fertility, but their unimproved counterparts did not take advantage of high nitrogen to produce grain. Furthermore, BSSS(R)C5 x BSCB1(R)C5 and BSSS(R)C7 x BSCB1(R)C7 demonstrated greater adaptation to high plant densities than did the other hybrids. Hybrids from the half-sib program were not adapted to high plant densities. Consequently, inbred lines tolerant of intermediate-to-high densities could be extracted from BSSS (R)C7 and BSCB1(R)C7, and inbreds that would respond efficiently to high rates of nitrogen fertilizer under low plant densities could be extracted from BS12C6, BSSS(R)C7, and BSCB1(R)C7.

Variety hybrids of the improved populations demonstrated greater abilities to produce grain at all rates of nitrogen fertilizer and plant density than did hybrids from the unimproved populations. Because lines recombined to form the improved populations were selected under higher rates of nitrogen and plant density than those in the original populations, we concluded that selection under high nitrogen fertilizer, high density environments resulted in superior performance at both low and high levels of these factors. If shortages of nitrogen fertilizer became severe, perhaps maize genotypes selected at high levels of this fertilizer would be more useful. Furthermore, in developing countries where fertilizer may not be readily available to the farmer, breeders might develop high-yielding genotypes by selecting under adequate rates of nitrogen. We should caution that our studies are preliminary and that extensive evaluations are needed before valid, general conclusions can be drawn about this subject. Studies conducted earlier (Russell, 1974; Duvick, 1976; Allan and Darrah, 1978), however, support our inferences.

Plant breeders are currently investigating the possibility of combining agronomic, morphological, and physiological traits into optimum plant types termed "ideotypes" (Donald, 1968; Mock and Pearce, 1975). Breeding crop ideotypes requires strong genetic associations between yield and the traits to be used in designing the ideotype. In an earlier report (Fakorede and Mock, 1978a), we used the unimproved and improved variety hybrids to obtain preliminary information for the maize ideotype proposed for central Iowa by Mock and Pearce (1975). In that study, we evaluated the changes in agronomic, morphological, and physiological traits associated with recurrent selection for grain yield. Kernel weight increased for BSSS(R)C7 x BSCB1(R)C7 relative to BSSS(R)C0 x BSCB1(R)C0, but not for hybrids from the half-sib program. Carbon-dioxide-exchange rate (CER, a measure of photosynthetic rate) did not change appreciably with recurrent selection. Leaf orientation

was significantly more upright for improved hybrids, but the changes were small, and the maize ideotype with upright leaves above and horizontal leaves below the ears was not obtained. Largest changes in other traits with selection for yield occurred during flowering and grain filling. Tassel size (i.e., number of branches and weight) and pollen-shed-to-silking interval decreased significantly for the improved hybrids and substantiated earlier conclusions (Mock and Buren, 1972; Buren et al., 1974; Mock and Pearce, 1975) that negative associations exist between grain yield and these traits. Also, silking dates were earlier for the improved hybrids. Furthermore, Fakorede and Mock (1978a) found that number of days to black-layer formation, grain-filling duration, and percentage of grain moisture at harvest were significantly higher in BSSS(R)C7 x BSCB1(R)C7 than in its unimproved counterpart. Leaf-area efficiency (i.e., grain per unit leaf area) was considerably higher for BS12C6 x B14A than for BS12C0 x B14A, and shelling percentage and harvest index demonstrated increasing trends as selection progressed.

In the present study, we investigated the effects of nitrogen fertilizer and plant density on changes in agronomic, morphological, and physiological traits associated with recurrent selection for yield. Similar to our earlier findings, we observed significant increases for leaf area, ear productivity, grain-yield components (although kernel weight did not change in the half-sib program), and dry-matter productivity in the improved relative to the unimproved hybrids. Also, lodging decreased and stalk quality improved significantly in the reciprocal recurrent selection program (Fakorede and Mock, 1978b).

These preliminary data indicate genetic associations between grain yield and many other traits in maize. Although several of these traits demonstrated desirable relationships with yield, poor agreement between observed and predicted correlated responses (Moll and Robinson, 1966; Moll and Stuber, 1974; Fakorede, 1977) suggested that maximum potentials for these traits were not attained via recurrent selection for grain yield *per se*. Perhaps use of index selection and ideotypes would alleviate this discrepancy and maximize grain yield in maize.

In another study, growth analysis was used to study dry-matter productivity and distribution by the unimproved and improved hybrids (Fakorede and Mock, 1980). Of all the growth traits studied, only leaf area, leaf-area duration, leaf-area index, and leaf-area-index duration were significantly larger in the improved than the unimproved hybrids. These differences usually occurred during grain filling; consequently, improved hybrids produced and translocated larger amounts of dry matter into the ear.

Our investigations led to the conclusion that the sink (i.e., ability of the grains to store photosynthate) more than the source (i.e., photosynthetic capacity) was limiting grain yield in BSSS(R) x BSCB1(R) and BS12. Evidently, increased grain yields that resulted from recurrent selection were consequences of longer duration of grain filling in BSSS(R) x BSCB1(R), and prolonged photosynthetic activity, increased production of photosynthate during grain filling, and increased translocation of photosynthate from the source to the sink in both BSSS(R) x BSCB1(R) and BS12.

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References

Acosta, A. E., and P. L. Crane. 1972. Further selection for lower ear height in maize. Crop Sci. 12:165-167.

Allan, A. Y., and L. L. Darrah. 1978. Effects of three cycles of reciprocal recurrent selection on the N and plant population responses of two maize hybrids in Kenya. Crop Sci. 18:112-114.

Arboleda-Rivera, F., and W. A. Compton. 1974. Differental responses of maize (*Zea mays* L.) to mass selection in diverse selection environments. Theor. Appl. Genet. 44:77-81.

Buren, L. L., J. J. Mock, and I. C. Anderson. 1974. Morphological and physiological traits in maize associated with tolerance to high plant density. Crop Sci. 14:426-429.

Chinwuba, P. V., C. O. Grogan, and M. S. Zuber. 1961. Interactions of detasseling, sterility, and spacing on yield of maize hybrids. Crop Sci. 1:279-280.

Cochran, W. G., and G. M. Cox. 1957. Experimental designs. John Wiley and Sons, Inc., New York.

Collins, W. K., W. A. Russell, and S. A. Eberhart. 1965. Performance of two-ear type of Corn Belt maize. Crop Sci. 5:113-116.

Comstock, R. E., and H. F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254-266.

Comstock, R. E., and H. F. Robinson. 1952. Estimation of average degree of dominance of genes. pp. 494-516. *In* J. W. Gowen (ed.) Heterosis. Iowa State University Press, Ames, Iowa.

Comstock, R. E., H. F. Robinson, and P. H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. Agron. J. 41:360-367.

Crosbie, T. M., R. B. Pearce, and J. J. Mock. 1978. Relationship between CO_2-exchange rate and plant traits in Iowa Stiff Stalk Synthetic maize population. Crop Sci. 18:87-90.

Crow, J. F. 1948. Alternative hypothesis of hybrid vigor. Genetics 33:477-478.

Crow, J. F. 1952. Dominance and over-dominance. pp. 282-297. *In* J. W. Gowen (ed.) Heterosis. Iowa State University Press, Ames, Iowa.

Darrah, L. L., S. A. Eberhart, and L. H. Penny. 1978. Six years of maize selection in 'Kitale Synthetic II,' 'Ecuador 573,' and 'Kitale Composite A' using methods of the comprehensive breeding system. Euphytica 27:191-204.

Donald, C. M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Duncan, E. R. 1954. Influence of varying plant population, soil fertility, and hybrid on corn yields. Soil Sci. Soc. Am. Proc. 18:437-440.

Duvick, D. N. 1958. Yields and other agronomic characteristics of cytoplasmically pollen-sterile corn hybrids, compared to their normal counterparts. Agron. J. 50:121-125.

Duvick, D. N. 1976. Genetic rates of gain in hybrid corn yields during the past 40 years. Am. Soc. Agron. Abstr. 1976:49-50.

East, E. M., and D. F. Jones. 1920. Genetic studies on the protein content of maize. Genetics 5.543-610.

Earley, E. B. 1965. Relative maximum yield of corn. Agron. J. 57:514-515.

Eberhart, S. A., S. Debela, and A. R. Hallauer. 1973. Reciprocal recurrent selection in the BSSS and BSCB1 maize populations and half-sib selection in BSSS. Crop Sci. 13:451-456.

El-Lakany, M. A., and W. A. Russell. 1971. Relationship of maize characters with yield in testcrosses of inbreds at different plant densities. Crop Sci. 11:698-701.

Evans, L. T. 1974. The physiological basis of crop yield. pp. 327-355. *In* L. T. Evans (ed.) Crop Physiology. Cambridge University Press, Cambridge.

Fakorede, M. A. B. 1975. Productivity of maize (*Zea mays* L.) as affected by plant density and simulated vertical leaf orientation. Unpublished M. S. Thesis. Iowa State University, Ames, Iowa.

Fakorede, M. A. B. 1977. Direct and correlated responses to recurrent selection for grain yield in maize breeding populations. Ph.D. Dissertation, Iowa State University. (Libr. Congr. Card No. Mic. 77-25983). University Microfilms. Ann Arbor, Mich. (Diss. Abstr. 38/06-B p. 2468).

Fakorede, M. A. B., and J. J. Mock. 1976. Leaf orientation and efficient utilization of solar energy by maize (*Zea mays* L.). WMO Symposium on Agrometeorology of the Maize Crop Proceedings. pp. 207-230.

Fakorede, M. A. B., and J. J. Mock. 1978a. Changes in morphological and physiological traits associated with recurrent selection for grain yield in maize. Euphytica 27:397-409.

Fakorede, M. A. B., and J. J. Mock. 1978b. Relationships between grain yield and agronomic traits in five maize variety hybrids. Iowa State J. Res. 52:355-360.

Fakorede, M. A. B., and J. J. Mock. 1978c. Yield stability and adaptation responses of maize variety hybrids developed by recurrent selection for grain yield. Maydica 23:89-100.

Fakorede, M. A. B., and J. J. Mock. 1980. Growth analysis of maize variety hybrids obtained from two recurrent selection programmes. New Phytol. 85:393-408.

Fakorede, M. A. B., N. N. Mulamba, and J. J. Mock. 1977. A comparative study of methods used for estimating leaf area of maize (*Zea mays* L.) from nondestructive measurements. Maydica 22:37-47.

Falconer, D. S. 1960. Introduction to quantitative genetics. The Ronald Press Co., New York.

Frankel, O. H. 1947. The theory of plant breeding for yield. Heredity 1:109-120.

Gardner, C. O. 1961. An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. Crop Sci. 1:241-245.

Grogan, C. O. 1956. Detasseling responses in corn. Agron. J. 48:247-249.

Hanway, J. J. 1971. How a corn plant develops. Iowa Coop. Ext. Serv. Spec. Rep. 48 (rev.).

Harris, R. E., C. O. Gardner, and W. A. Compton. 1972. Effects of mass selection and irradiation in corn measured by random S_1 lines and their testcrosses. Crop Sci. 12:594-598.

Hayes, H. K., and R. J. Garber. 1919. Synthetic production of high protein corn in relation to breeding. J. Am. Soc. Agron. 11:309-318.

Horner, E. S., H. W. Lundy, M. C. Lutrick, and R. W. Wallace. 1963. Relative effectiveness of recurrent selection for specific and for general combining ability in corn. Crop Sci. 3:63-66.

Horner, E. S., H. W. Lundy, M. C. Lutrick, and W. H. Chapman. 1973. Comparison of three methods of recurrent selection in maize. Crop Sci. 13:485-489.

Horner, E. S., M. C. Lutrick, W. H. Chapman, and F. G. Martin. 1976. Effect of recurrent selection for combining ability with a single-cross tester in maize. Crop Sci. 16:5-8.

Hull, F. H. 1945. Recurrent selection for specific combining ability in corn. J. Am. Soc. Agron. 37:134-145.

Jenkins, M. T. 1940. The segregation of genes affecting yield of grain in maize. J. Am. Soc. Agron. 32:55-63.

Jinahyon, S., and W. A. Russell. 1969. Effects of recurrent selection for stalk-rot resistance on other agronomic characters in an open-pollinated variety of maize. Iowa State J. Sci. 43:239-251.

Lang, A. L., J. W. Pendleton, and G. H. Dungan. 1956. Influence of population and nitrogen levels on yield and protein and oil contents of nine corn hybrids. Agron. J. 48:284-289.

Lerner, I. M. 1958. The genetic basis of selection. John Wiley and Sons, Inc., New York.

Lonnquist, J. H. 1961. Progress from recurrent selection procedures for the improvement of corn populations. Nebr. Agric. Exp. Stn. Res. Bull. 197.

Lonnquist, J. H. 1967. Mass selection for prolificacy in maize. Züchter 37:185-188.

McVicker, M. H., and G. M. Shear. 1946. Variation in response of different varieties and hybrids of field corn to planting rate. J. Am. Soc. Agron. 38:933-935.

Meyer, D. W. 1970. Use of male sterility for increasing the population tolerance of corn (*Zea mays* L.). Ph.D. Dissertation. Iowa State University. (Libr. Congr. Card No. Mic. 70-25808). University Microfilms. Ann Arbor, Mich. (Diss. Abstr. 31/06-B p. 3113).

Mock, J. J., and L. L. Buren. 1972. Classification of maize (*Zea mays* L.) inbreds for population tolerance by general combining ability. Iowa State J. Sci. 46:395-404.

Mock, J. J., and R. B. Pearce. 1975. An ideotype of maize. Euphytica 24:613-623.

Moll, R. H., and H. F. Robinson. 1966. Observed and expected response in four selection experiments in maize. Crop Sci. 6:319-324.

Moll, R. H., and C. W. Stuber. 1971. Comparisons of response to alternative selection procedures initiated with two populations of maize (*Zea mays* L.). Crop Sci. 11:706-711.

Moll, R. H., and C. W. Stuber. 1974. Quantitative genetics: Empirical results relevant to plant breeding. Adv. Agron. 26:277-313.

Montgomery, E. G. 1911. Correlation studies in corn. Nebr. Agric. Exp. Stn. Annu. Rep. 24:108-159.

Mooers, C. A. 1933. The influence of soil productivity on the order of yield in a varietal trial in corn. J. Am. Soc. Agron. 25:796-800.

Murata, Y. 1968. Physiological responses to nitrogen in plants. pp. 235-262. *In* R. C. Dinauer (ed.) Physiological aspects of crop yield. Am. Soc. Agron., Madison, Wisconsin.

Noble, S. W., and W. A. Russell. 1963. Effects of male-sterile cytoplasm and pollen fertility restorer genes on performance of hybrid corn. Crop Sci. 3:92-96.

Nunez, R., and E. Kamprath. 1969. Relationship between N response, plant population and row width on growth and yield of corn. Agron. J. 61:279-282.

Obilana, A. T., and A. R. Hallauer. 1974. Estimation of variability of quantitative traits in BSSS by using unselected maize inbred lines. Crop Sci. 14:99-103.

Pearce, R. B., J. J. Mock, and T B. Bailey. 1975. Rapid method for estimating leaf area per plant in maize. Crop Sci. 15:691-694.

Pendleton, J. W., G. E. Smith, R. S. Winter, and T. J. Johnston. 1968. Field investigation of the relationships of leaf angle in corn (*Zea mays* L.) to grain yield and apparent photosynthesis. Agron. J. 60:422-424.

Penny, L. H., W. A. Russell, and G. F. Sprague. 1962. Types of gene action in yield heterosis in maize. Crop Sci. 2:341-344.

Penny, L. H., W. A. Russell, and A. R. Hallauer. 1963. Recurrent selection. pp. 352-367. *In* W. D. Hanson and H. F. Robinson (eds.). Statistical genetics and plant breeding. Natl. Acad. Sci.-Natl. Res. Counc. Publ. 982. Washington, D.C.

Pepper, G. E. 1974. The effect of leaf orientation and plant density on the yield of maize (*Zea mays* L.). Ph.D. Dissertation. Iowa State University. (Libr. Congr. Card No. Mic. 75-10500). University Microfilms. Ann Arbor, Mich. (Diss. Abstr. 35/11-B p. 5234).

Pepper, G. E., R. B. Pearce, and J. J. Mock. 1977. Leaf orientation and yield of maize. Crop Sci. 17:883-886.

Powell, R. D. 1968. The yield, growth, and chemical composition of corn as influenced by hybrids and high rates of nitrogen, phosphorus, and potassium fertilizers. Ph.D. Dissertation. Iowa State University. (Libr. Congr. Card No. Mic. 68-14815). University Microfilms. Ann Arbor, Mich. (Diss. Abstr. 29/04-A p. 1238).

Rehm, G. W., R. C. Sorenson, and W. J. Moline. 1976. Time and rate of fertilizer application for seeded warm-season and bluegrass pastures. I. Yield and botanical compositions. Agron. J. 68:759-764.

Robinson, H. F., R. E. Comstock, and P. H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. Agron. J. 41:353-359.

Russell, W. A. 1968. Testcrosses of one- and two-ear types of Corn Belt maize inbreds. I. Performance at four plant stand densities. Crop Sci. 8:244-247.

Russell, W. A. 1969. Hybrid performance of maize inbred lines selected by testcross performance in low and high plant densities. Crop Sci. 9:185-188.

Russell, W. A. 1974. Comparative performance for maize hybrids representing different eras of maize breeding. Proc. Corn and Sorghum Res. Conf. 29:81-101.

Russell, W. A., and S. A. Eberhart. 1968. Testcrosses of one- and two-ear types of Corn Belt maize inbreds. II. Stability of performance in different environments. Crop Sci. 8:248-251.

Russell, W. A., and C. L. Prior. 1975. Stability of yield performance of nonprolific and prolific maize hybrids. Iowa State J. Res. 50:17-27.

Russell, W. A., and A. H. Teich. 1967. Selection in *Zea mays* L. by inbred line appearance and testcross performance in low and high plant densities. Iowa Agric. Home Econ. Exp. Stn. Res. Bull. 552:919-946.

Russell, W. A., S. A. Eberhart, and U. A. Vega O. 1973. Recurrent selection for specific combining ability for yield in two maize populations. Crop Sci. 13:257-261.

Schwanke, R. 1965. Alteration of reproductive attributes of corn varieties by population and detasseling. Ph.D. Dissertation. Iowa State University. (Libr. Congr. Card No. Mic. 66-3008). University Microfilms. Ann Arbor, Mich. (Diss. Abstr. 26/09 p. 4921).

Shibles, R. M., and C. R. Weber. 1966. Interception of solar radiation and dry matter production by various soybean planting patterns. Crop Sci. 6:55-59.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical methods. Iowa State University Press, Ames, Iowa.

Sprague, G. F., and S. A. Eberhart. 1977. Corn and corn improvement. Am. Soc. Agron., Madision, Wisconsin.

Sprague, G. F., and P. A. Miller. 1950. A suggestion for evaluating current concepts of the genetic mechanism of heterosis in corn. Agron. J. 42:161-162.

Sprague, G. F., W. A. Russell, and L. H. Penny. 1959. Recurrent selection for specific combining ability and type of gene action involved in yield heterosis in corn. Agron. J. 51:392-394.

Steel, R. G. D., and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York.

Walejko, R. N., and W. A. Russell. 1977. Evaluation of recurrent selection for specific combining ability in two open-pollinated maize cultivars. Crop Sci. 17:647-651.

Wigan. L. G., and K. Mather. 1942. Correlated response to the selection of polygenic characters. Ann. Eugen. 11:354-364.

Winter, S. R., and A. J. Ohlrogge. 1973. Leaf angle, leaf area, and corn (*Zea mays* L.) yields. Agron. J. 65:395-397.

Woolley, D. G., N. P. Baracco, and W. A. Russell. 1962. Performance of four corn inbreds in single-cross hybrids as influenced by plant density and spacing patterns. Crop Sci. 2:441-444.

Wright, S. 1921. Systems of mating. Genetics 6:111-178.

Wright S. 1935. The analysis of variance and the correlation between relatives with respect to deviations from an optimum. J. Genet. 30:243-356.


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